

ON THE QUANTITATIVE EXPLANATION OF STOMATAL TRANSPIRATION

BY

G. G. J. BANGE

Botanical Institute of the University of Leyden, Netherlands

(Received June 30th, 1953)

CONTENTS

I. INTRODUCTION	
A. The question of stomatal regulation	255
B. The diffusion resistance.	256
C. The influence of wind	265
II. MATERIAL AND METHODS	
A. Selection of the test plant.	268
B. Determination of stomatal transpiration in still air and in wind.	268
C. Determination of stomatal aperture	270
D. Determination of evaporation in still air	271
E. Evaluation of the experimental data	271
III. EXPERIMENTAL RESULTS.	272
IV. DISCUSSION	279
SUMMARY.	280
APPENDIX.	280
I. Calculation of the diffusion resistance in the substomatal cavity	280
II. Calculation of the diffusion resistance in the stoma	286
III. Calculation of the diffusion resistance within a vapour shell of limited size	289
IV. Theoretical analysis of the experiments on models by SIERP and SEYBOLD (1929)	290
V. Theoretical analysis of the experiments on models by HUBER (1930)	293
VI. Calculation of the correction for the number of stomata per cm ²	295
ACKNOWLEDGEMENT	296
REFERENCES.	296

I. INTRODUCTION

A. *The question of stomatal regulation*

The study of leaf anatomy and of the mechanism of the opening and closing of stomatal guard cells leads one to suppose that the stomata constitute the main or even the sole regulating system in leaf transpiration. Nevertheless this supposition has been questioned on other grounds by many authors.

One might say that the classical work of BROWN and ESCOMBE (1900) on evaporation and gaseous exchange through porous films contained one of the main sources of doubt. As is well known these investigators stated that the transpiration in leaves of *Helianthus annuus* L. was 6 times smaller than they had expected from their theoretical considerations, so that, apart from the stomata, it would seem that other factors have a profound influence on the transpiration rate.

Subsequently this idea was corroborated by several other investigators. LIVINGSTON (1906), expressing his results in terms of relative transpiration to eliminate the influence of environmental factors, found the daily maximum of transpiration occurred before that of evaporation. He did not consider the stomata responsible for the fact that both maxima do not coincide, because the phenomenon appeared before any stomatal closure was to be expected. LLOYD (1908), finding very little correlation between transpiration rate and stomatal aperture, concluded that the stomata influence the transpiration only at their smallest apertures. LIVINGSTON and BROWN (1912), obtaining results similar to those of LIVINGSTON (1906), put forward the theory that, as a consequence of the water loss from the leaf, an incipient drying of the cell walls lining the intercellular spaces should cause an additional resistance to transpiration. The same conclusion was drawn by SHREVE (1914) from similar experiments. TRELEASE and LIVINGSTON (1916), using the porometer method, found that in the course of the day the maximum of stomatal aperture was reached some hours after the maximum of transpiration, so that another mechanism seemed to play a role in regulating transpiration. KNIGHT (1917, 1922) also accepted a dual influence on the transpiration rate: — the incipient drying of the cell walls would control it in case of bright weather and wide open stomata, while at low light intensities and small apertures the stomata themselves would be the main controlling factor.

However, not all the English and American authors were of the same opinion. DARWIN (1916) stated a reasonable parallelism between transpiration rate and stomatal aperture. LOFTFIELD (1921) concluded from his experiments that the stomata regulate the transpiration to a great extent, although in his opinion at more than 50 % of the maximal aperture evaporation factors become more important than the stomata.

Evidently the scepticism among the authors cited as to the controlling power of stomata mainly concerned the greater apertures. The question arises as to whether this scepticism was justified.

B. *The diffusion resistance*

BROWN and ESCOMBE based their theoretical considerations on Fick's diffusion law, one expression of which is as follows: —

$$m/t = k \cdot (c - c') \cdot O/l$$

(m = quantity of matter diffusing through a tube in time t ,
 l = length of tube,

- O = sectional area of tube,
 c, c' = concentration of matter at beginning and end of tube,
 k = diffusion constant, the value of which depends on the quality of the diffusing substance and of the diffusion medium and on the temperature).

It is easily seen that this diffusion law represents an analogue of Ohm's law for the conduction of electricity through a homogeneous conductor, the expression of which is

$$\frac{e}{t} = f \cdot (v - v') \cdot \frac{O}{l} = \frac{v - v'}{1/f \cdot l/O} = \frac{v - v'}{r}$$

- e = quantity of electricity flowing through a conductor in time t ,
 l = length of conductor,
 O = sectional area of conductor,
 v, v' = electrical potential at beginning and end of conductor,
 f = conductivity constant, the value of which depends on the quality of the conducting material and on the temperature,
 r = electrical resistance of conductor).

As a consequence we may define the diffusion resistance as an analogue of the electrical resistance and represent it by

$$r = 1/k \cdot l/O.$$

For a number of conductors in series Ohm's law reads

$$\frac{e}{t} = i = \frac{v - v'}{r + r' + r'' + r''' + \dots} = \frac{v - v'}{R}$$

- i = strength of current,
 $v - v'$ = total potential difference,
 R = total resistance of the series equalling the algebraic sum of the separate resistances r, r', r'', r''' etc.).

As Ohm's law for electrical currents and Fick's law for diffusion are completely analogous in the case of single conductors, there is no reason why this analogy should not be extended to the case of a series of conductors. Thus, with the assumption of a steady state, the formula for the diffusion rate through a series of tubes becomes

$$\frac{m}{t} = i = \frac{c - c'}{r + r' + r'' + r''' + \dots} = \frac{c - c'}{R}$$

- i = diffusion rate,
 $c - c'$ = total concentration difference,
 R = total diffusion resistance of the series equalling the algebraic sum of the separate resistances r, r', r'', r''' etc.).

Our problem therefore is greatly simplified by the facts that

1. only concentrations c and c' at the beginning and end of the diffusion path are needed for the calculation of the diffusion rate and the intermediate ones are not required;

2. the total diffusion resistance in a heterogeneous system may be obtained by simple addition of the respective resistances of the component parts. One may call this the "principle of successive resistances". This principle has already been applied by several authors in different cases, e.g. by BROWN and ESCOMBE (1900) and RENNER (1910) to transpiration and by PENMAN and SCHOFIELD (1951) also to carbon dioxide assimilation.

This formulation of Fick's law, however, is only applicable if, in the system used, the surfaces of equal vapour concentration are flat and therefore the diffusion lines perpendicular to these surfaces are parallel lines. These conditions are not satisfied in the case of a circular evaporating surface lying in a flat non-evaporating plane (fig. 1). Theoretical deductions (STEFAN 1881) have shown that in

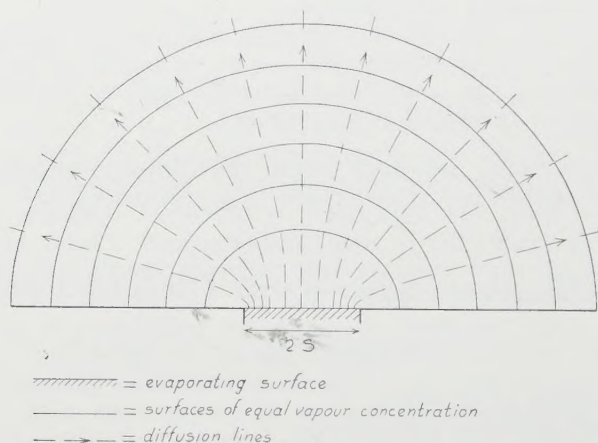


Fig. 1. Diffusion lines and surfaces of equal vapour concentration over a circular evaporating surface lying in a flat non-evaporating plane.

this case the surfaces of equal vapour concentration are halved oblate spheroids (formed by rotating the upper half of an ellipse about its short axis) and that the diffusion lines are hyperbolas, the focal circles, respectively the foci coinciding with the margin of the evaporating surface.

In this system STEFAN and later BROWN and ESCOMBE calculated the diffusion resistance to be

$$r = 1/k \cdot 1/4s$$

(s = radius of evaporating surface). According to this formula, which only holds for absolutely still air, the evaporation rate is proportional to the radius of the surface (Stefan's diameter law).

Additional resistances are introduced if a septum perforated by circular pores is placed over such an evaporating surface (fig. 2). In this case the total diffusion resistance will consist of three different parts, viz: —

1. The resistance in the pores

$$r_p = 1/k \cdot l/\pi s_1^2 \cdot 1/N$$

(s_1 = radius, l = depth and N = number of pores).

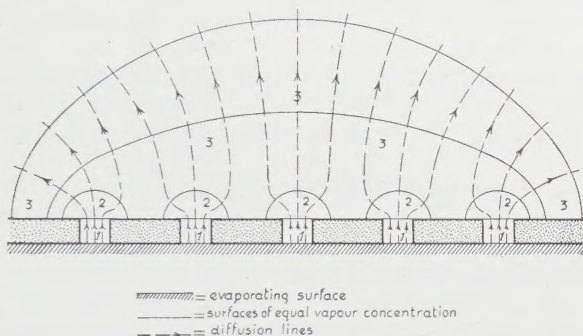


Fig. 2. Diffusion lines and surfaces of equal vapour concentration over an evaporating surface over which a perforated septum has been placed.

2. The resistance in the micro vapour cups over the individual pores, amounting to

$$r_{d1} = 1/k \cdot 1/4s_1 \cdot 1/N.$$

3. The resistance in the macro vapour cup over the entire septum. Its value is

$$r_{d2} = 1/k \cdot 1/4s_2$$

(s_2 = radius of septum).

Therefore the total diffusion resistance of this system will be

$$R = r_p + r_{d1} + r_{d2} = \frac{1}{k} \cdot \left(\frac{1}{N} \cdot \left(\frac{l}{\pi s_1^2} + \frac{1}{4s_1} \right) + \frac{1}{4s_2} \right).$$

If in a transpiring leaf one assumes a saturated water vapour concentration in the substomatal spaces and pays due consideration to the elliptical shape of the pores, it may be considered as comparable to the above system.

BROWN and ESCOMBE developing their formulae in this way made calculations which proved to agree fairly well with the results of their experiments with models. They also tried to compute the rate of water loss from a leaf of *Helianthus annuus*, but due to an oversight they omitted the evaluation of the macro vapour cup over the leaf. Consequently the remaining resistance calculated was too low and the theoretical transpiration rate derived from it became several times greater than the one observed. Much confusion would have been avoided, if they had not made this small omission, which apparently caused several authors to accept an additional transpiration resistance inside the leaf.

As RENNER pointed out clearly as early as 1910, neglect of the macro vapour cup leads to the preposterous conclusion that, if a perforated septum be placed over a free water surface, the evaporation rate should be increased.

The formula derived by STEFAN and BROWN and ESCOMBE for the diffusion resistance over a circular evaporating surface theoretically applies only if the vapour cup is of unlimited size. Obviously this will never be the case as "still air" is never quite still and the vapour cup is always more or less disturbed by convection currents. It is impossible, however, to evaluate theoretically the degree of this disturbance.

Nevertheless if the total diffusion resistance is to be calculated for leaf transpiration, it is necessary to obtain the real value of the resistance in the macro vapour cup. VAN DEN HONERT (1948) pointed out that this resistance may be represented by that of a hypothetical, completely still air layer of a certain thickness over the transpiring surface. On the outside this hypothetical air layer is thought to be bordered by air which is continuously renewed and which has the same water vapour concentration as the rest of the surrounding air. Its diffusion resistance may be determined empirically, in any particular case, by measuring the evaporation rate from a free water surface of exactly the same shape and under the same conditions as the object. The thickness of this air layer depends on the degree of air convection and may be calculated using the diffusion constant of water vapour in air and applying Fick's law. In still air this may amount to anything from several mm to one cm depending on the diameter of the evaporating surface.

We are well aware that a rather simplified conception of the conditions is involved in the assumption of a rigid air layer of a certain thickness. Meanwhile, WELTEN (1933) using cobalt paper showed that there are actually vapour cups of the same order of thickness over evaporating surfaces, so there is no doubt that, at least in still air, a considerable diffusion resistance outside the leaf actually occurs.

So the total diffusion resistance in a leaf may be calculated by addition of the three successive diffusion resistances which the water vapour has to pass, viz: —

1. The resistance in the stomata. If the latter are represented by cylindrical tubes with an elliptical section, this resistance per cm^2 leaf surface amounts to

$$r_s = 1/k \cdot l/\pi ab \cdot 1/N$$

(l = length of tube,

a = half the short axis of the ellipse,

b = half the long axis of the ellipse,

N = number of stomata per cm^2 leaf surface).

With variation of the stomatal aperture only the short axis is considered to be variable. This is not far from reality.

2. The resistance in the micro vapour cups over the individual

stomata. The total resistance per cm^2 leaf surface of these vapour cups may be calculated by BROWN and ESCOMBE's formula

$$r_d = 1/k \cdot 1/4\sqrt{ab} \cdot 1/N$$

(\sqrt{ab} = radius of the circle with an area equal to the elliptical section of the stoma).

3. The resistance in the macro vapour cup over the whole surface of the leaf (= the hypothetical still air layer). Its value may be derived from the evaporation rate in the way already described.

For the sake of simplicity we will for the moment leave out of account the resistance 2 as being of minor importance. In this case the total resistance consists of two, mutually independent, partial resistances. The stomatal resistance r_s is variable and inversely proportional to the stomatal aperture while that of the macro vapour cup or still air layer, which we call A , is constant.

The diffusion rate i may now be computed

$$i = (c - c') / (r_s + A)$$

(c = concentration of water vapour in the substomatal space,
 c' = concentration of water vapour in the surrounding air).

As long as r_s is large compared to A , that is with small apertures, r_s will practically determine the transpiration rate and the transpiration will be approximately proportional to the stomatal aperture. However, the greater the aperture, the more important A becomes and eventually it may constitute the main limiting factor in transpiration. Consequently the curve representing the relation between the stomatal aperture and the transpiration rate in still air (fig. 3) will have an initial steep part, but will gradually flatten.

RENNER as early as 1910 had already shown a clear insight into

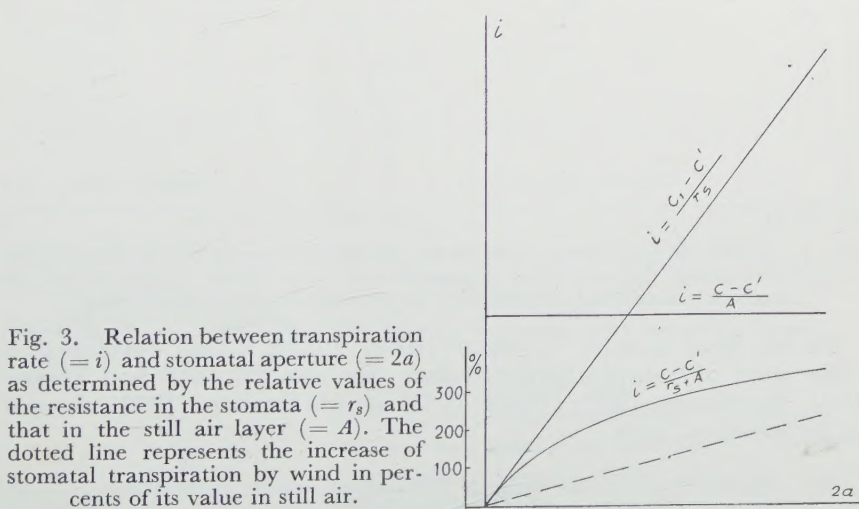


Fig. 3. Relation between transpiration rate ($= i$) and stomatal aperture ($= 2a$) as determined by the relative values of the resistance in the stomata ($= r_s$) and that in the still air layer ($= A$). The dotted line represents the increase of stomatal transpiration by wind in percents of its value in still air.

these principles; as mentioned earlier he was the one to detect the flaw in BROWN and ESCOMBE's calculation of stomatal transpiration. He also disputed LLOYD's conclusion that stomata have no regulating influence at greater apertures and found a fairly good agreement between the transpiration rates calculated theoretically and those actually determined.

LARMOR (1918) again brought forward a similar point of view. It is surprising that the later German and Swiss workers did not use and extend these principles. SEYBOLD's (1929*a* and *b*) theoretical considerations therefore remained rather unprofitable. SIERP and SEYBOLD (1927 and 1929) determined evaporation rates through perforated brass septa and in their opinion these did not agree with those calculated by means of BROWN and ESCOMBE's formula. From these results they concluded that in practice the principles developed by BROWN and ESCOMBE were not valid for pores of the order of magnitude of the stomata. That this conclusion was a little premature may appear from fig. 4 A and B. In this figure SIERP and SEYBOLD's data concerning the relation between pore diameter and relative evaporation rate are compared with the results of a theoretical analysis of their experiments according to the principle of successive resistances (see Appendix, part IV). The agreement is so close that these experiments might even be used as an empirical proof of how well the foregoing principle applies.

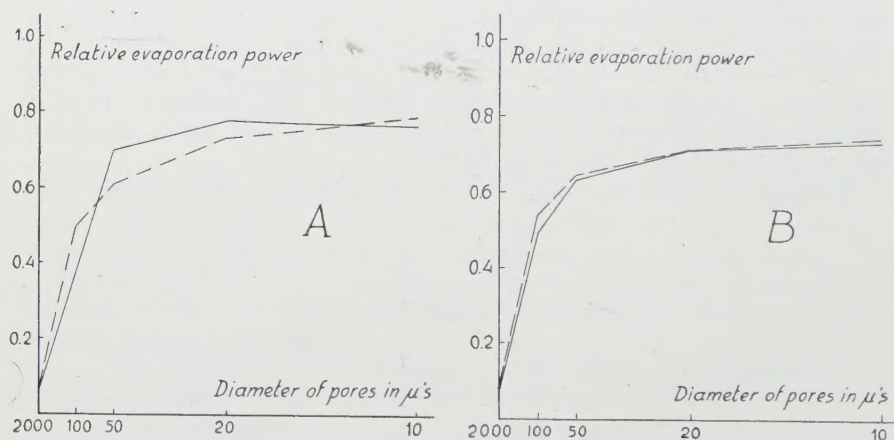


Fig. 4. SIERP and SEYBOLD's curves for the relation between pore size and relative evaporation power (drawn lines) compared with the results of our theoretical analysis (dotted lines). A. No filter paper used. B. Filter paper used.

In his later articles SEYBOLD (1930, 1931*a*, 1934) developed a conception of transpiration resistance (see also SEYBOLD and FÜSSER 1931, BACHMANN 1932, FÜSSER 1933) which BREWIG (1933) showed to be identical with

$$w = \frac{p_{\max} - p_0}{p_s - p_0}$$

(p_{\max} = saturated water vapour pressure at leaf temperature,
 p_s = water vapour pressure at leaf surface,
 p_o = water vapour pressure of surrounding air).

Where in our terms $\text{Evaporation} = (p_{\max} - p_o)/r_{\text{air layer}}$ and $\text{Transpiration} = (p_s - p_o)/r_{\text{air layer}}$ it is clear that, as MAXIMOV (1931) and WELTEN (1933) rightly remarked, such a conception of transpiration resistance is nothing but the reciprocal value of LIVINGSTON'S (1906) relative transpiration T/E , provided evaporation and transpiration are measured under comparable conditions (same value of $r_{\text{air layer}}$).

WELTEN'S (1933) formula of transpiration resistance

$$W_s = W_1/f + W_2$$

(W_s = total transpiration resistance,

W_1 = part of resistance that is inversely proportional to width of stomatal slit,

W_2 = part of resistance that is independent of width of stomatal slit,
 f = transpiring area)

has the advantage, as MONSI (1944) observed, of consisting of one part varying with stomatal aperture and another independent of it. MONSI therefore could show it to be identical with RENNER'S conception of transpiration resistance.

HUBER'S (1930) experiments with perforated septa deserve special consideration. He gave a qualitative explanation of his results by means of the conception of "mutual interference of pores" and expressed his empirical "interference law" in a mathematical formula.

The conception of interference hardly lends itself to quantitative considerations, although VERDUIN (1947) made such an attempt.

The mutual interference of pores is brought about by the diffusion lines, which radiate out from the pores at first, becoming parallel

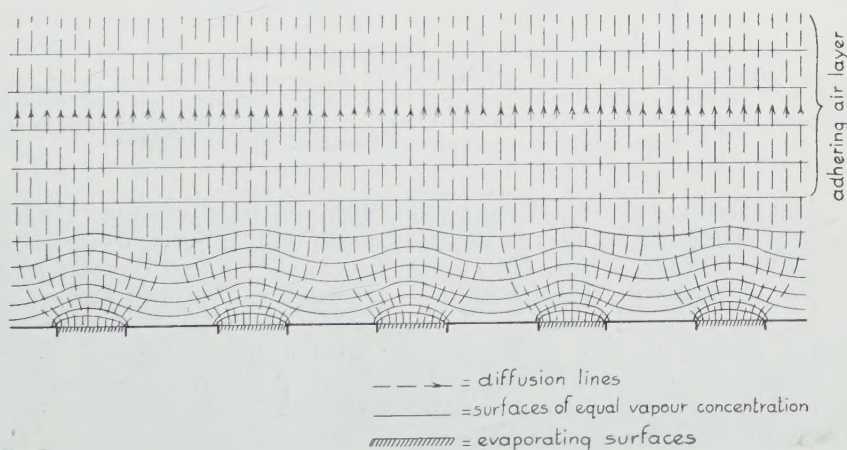


Fig. 5. Transition of micro vapour cups in adhering air layer (mutual interference of pores).

to each other and perpendicular to the surface. It should be stressed that there is essentially no difference between this conception and the view developed in this paper. That section where the lines become parallel is to be regarded as an adhering air layer forming an external resistance (fig. 5).

Again, HUBER's curves can be explained quantitatively in terms of successive resistances. In fig. 6 the relation between the total pore surface and the relative evaporation rate of septa with pores of 1 mm^2 and $2000 \mu^2$, as empirically determined by HUBER, is represented by a continuous line, whereas the corresponding theoretical values are given by a dotted line (for the calculation see Appendix, part V). The agreement between theory and experiment appears to be satisfactory.

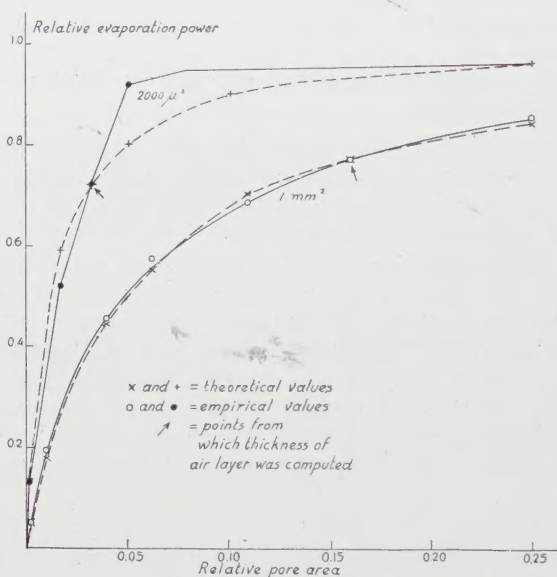


Fig. 6. HUBER's curves for the relation between relative pore area and relative evaporation power of septa with pores of 1 mm^2 and $2000 \mu^2$ (drawn lines) compared with the results of our theoretical analysis (dotted lines).

The relation between stomatal aperture and transpiration rate has been investigated by no one more carefully and thoroughly than by STÅLFELT (1932a, 1935). His curves (fig. 7) — the first of their kind in the literature on transpiration — are steep at first, but flatten off at greater stomatal apertures. In explaining his results STÅLFELT too based himself on the conception of mutual interference of pores. VAN DEN HONERT (1948) pointed out that, if the transpiration rate is mainly determined by a variable resistance in the stomata and a constant resistance in the adhering air layer, a similar shape of the curve is to be expected (cf fig. 3).

MONSI (1944) also found curves of this shape and tested them by

RENNER's formulae. There was some agreement between theory and experiment.

GÄUMANN and JAAG (1938) in their theoretical derivation of the transpiration rate thought in terms of water vapour effusion instead

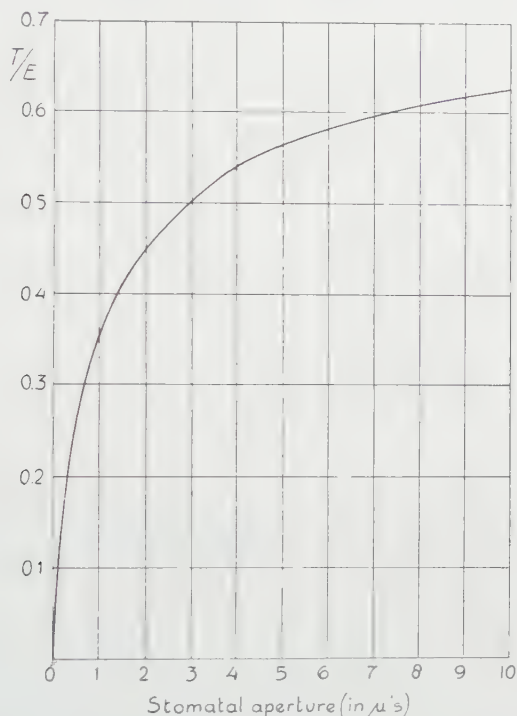


Fig. 7. STÅLFELT's curve for the relation between relative transpiration ($= T/E$) and stomatal aperture in still air (*Betula pubescens*).

of diffusion and applied Poiseuille's law. It is difficult to see how there can be a gas-stream through the stomata except in anomalous cases.

C. The influence of wind

The question arises as to which relation is to be expected between transpiration rate and stomatal aperture in wind.

The rate of evaporation from a free water surface is greatly increased by wind. This may safely be attributed to the partial elimination of the diffusion resistance in the macro vapour cup or, in other words, to the decrease in the thickness of the adhering air layer. In a leaf where the macro vapour cup and the micro ones have been blown away and so the external resistance has been reduced to a negligible value, the only remaining resistance is that inside the leaf. The greater part of it is that in the stomata which, as has been shown (page 260), equals

$$r_s = 1/k \cdot l/\pi ab \cdot 1/N.$$

Accordingly in wind the transpiration rate should be directly proportional to the stomatal aperture (fig. 3), at least if the wind is strong enough to blow away all external diffusion resistances. For small leaf areas this seems to be the case even at low wind velocities, as STÅLFELT (1932*b*) found that for a leaf area of 25 cm² wind of a velocity as low as 0.5 m/sec is sufficient to effect a maximum increase of transpiration (fig. 8). The experience that fairly low wind velocities suffice for blowing dust from a smooth surface accords with this statement.

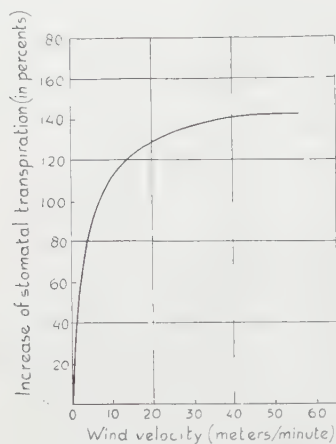


Fig. 8. STÅLFELT's curve for the relation between the increase of stomatal transpiration by wind and the wind velocity.

From the foregoing it will be clear that the measure of increase of transpiration by wind is largely independent of the stomatal aperture. The greater the aperture and so the smaller the stomatal resistance, the greater the relative value of the external resistance which is blown away and so the greater the effect to be expected (fig. 3). Failure to appreciate this is certainly one of the main causes of the controversies concerning the influence of wind on transpiration. A few opinions may be mentioned.

WIESNER (1887) stated that transpiration may be largely increased by wind.

RENNER (1910) had found some quantitative agreement between transpiration rates measured in wind and the respective values calculated according to the principles described.

SEYBOLD (1929*a* and *b*, 1931*b*), however, was of the opinion that in still air convection currents are sufficiently strong to eliminate the micro vapour cups over the stomata so that wind could not increase stomatal transpiration. He attributed any observed increase of transpiration by wind to an increase of cuticular transpiration.

FIRBAS (1931) found in most cases an increase of transpiration by wind.

The same was found by STÅLFELT (1932*b*, 1935). Again he was the first (1935) to publish a curve representing the relation between stomatal aperture and transpiration rate in wind (fig. 9). The relation

is nearly linear as STÅLFELT expected, as in this case no interference of pores would occur.

WRENGER (1935, 36) concluded from her experiments that in xeromorphic plants wind has less influence on the transpiration rate

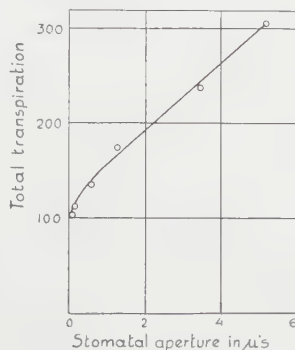


Fig. 9. One of STÅLFELT's curves for the relation between transpiration rate and stomatal aperture in wind (*Avena sativa*).

than in mesomorphic plants and that its influence is greater with larger stomatal apertures. These results are entirely in accordance with our theory.

The experiments of GÄUMANN and JAAG (1939*a* and *b*) have the drawback that the aperture of the stomata was considered to be a linear function of the light intensity which according to STÅLFELT's (1927, 1929) results is hardly justified.

SEYBOLD's opinion that evaporation through pores of stomatal size is not enhanced by wind was founded on the results of his own (1929*a*) experiments with porous septa and those of SIERP and SEYBOLD (1929). However, it is subject to serious doubt if this conclusion was justified. Similar experiments by HUBER (1930) showed that the closer the pores, the less evaporation through the septum differs from free evaporation in wind and that the total poral area is far more important in determining the effect of wind than the diameter of the pores at constant poral area. These results fit completely into our theory.

A review of the literature leads to the conclusion that the work of BROWN and ESCOMBE and of RENNER seemed to open the way to a quantitative explanation of stomatal transpiration as a diffusion process in a system of successive variable resistances. However, the further elaboration necessary and the completion of their principles failed to appear, so their practical applicability was questioned and explanations of an other kind were sought.

The purpose of the following experiments was to investigate whether stomatal transpiration can be explained quantitatively as a diffusion process of water vapour in air in a system of successive variable resistances. The experiments and the conclusions to which they led are described in the following chapters. The mathematical analysis of the diffusion resistances and other calculations will be given in the Appendix.

II. MATERIAL AND METHODS

A. Selection of the test plant

Zebrina pendula Schnizl. was chosen as a test plant. The reason was that this species has relatively large stomatal pores (mean long axis 35μ) with deep substomatal spaces (fig. 10), consequently under the microscope the image of the underlying cells does not interfere with that of the pores and the apertures can be measured without using an immersion oil as recommended by STÅLFELT (1929a) for *Betula*, *Vicia* etc.. *Zebrina* has been used by other workers (PAETZ 1930) for the same reason.



Fig. 10. Transverse section through a stoma of *Zebrina pendula* (s = guard cell, b = accessory cell, a = substomatal cavity, i = intercellular space, sp = spongy parenchyma, e = epidermal cell).

B. Determination of stomatal transpiration in still air and in wind

The transpiration rate is expressed in terms of grams of water vapour given off by 1 cm^2 leaf surface per second at a concentration difference corresponding to 1% saturation deficit. It was determined by measuring the loss of weight of a leaf disc during a given time on an air damped balance.

To obtain comparable results two factors should be constant, viz: —

1. The surface of the leaf disc, as the size of the macro vapour cup (thickness of the adhering air layer) depends on the size of the leaf disc.
2. The temperature of the leaf disc.

A constant leaf surface was obtained by punching out discs from *Zebrina* leaves with a diameter of $\pm 2.8\text{ cm}$. The punch (fig. 11A) consisted of a brass cylinder (a) with a rubber stopper (b) inside it which was used to hold two razor blades (c) in a circular position adjacent to the metal cylinder. The cut was made in such a way that the mid-rib passed approximately through the centre of the disc. Evaporation from the cut margin was eliminated by putting the leaf disc into a holder. Fig. 11B shows this leaf holder which consisted of

a short brass cylinder (d) closed at the top and with rounded edges. The leaf disc (e) is put on top of this cylinder and then a thin rubber ring (f) of the same external diameter is placed over it. This in turn is covered by a brass cap (g) which is almost completely open at the top but just covers the rubber ring. Paraffin wax (h) is used to seal the space between this cap and the cylinder round the side. The remaining free area of the leaf disc measured exactly 5 cm^2 .

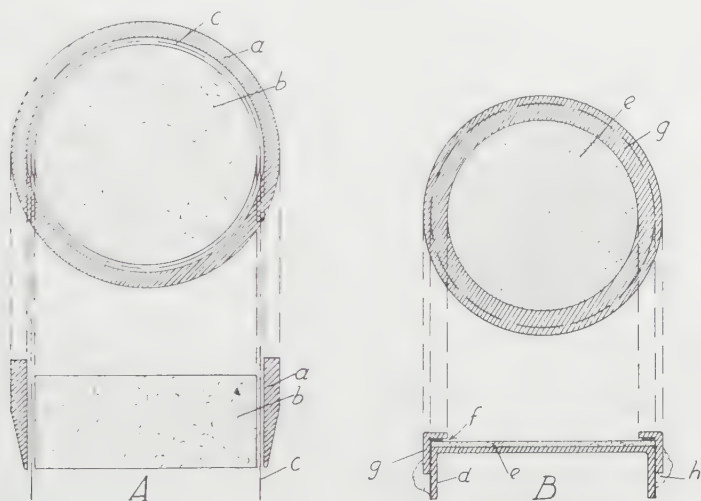


Fig. 11. A. Leaf punch. B. Leaf holder. Explanation in the text.

This method had the additional advantage that the transpiration of the upper and lower sides of the leaf disc could be estimated separately.

The cooling effect of transpiration is difficult to evaluate, therefore we tried to eliminate it, as far as possible, in the following way: —

1. Before the transpiration measurement the leaf disc in its holder was covered by a watch glass in order to bring it into temperature equilibrium with its environment. The weighing began about 10 seconds after removal of the watch glass which time can be computed to suffice amply in most cases for filling up the adhering air layer with water vapour and so reaching a steady state of evaporation or transpiration. In cases of very low transpiration rates the inaccuracy introduced was eliminated by taking the weighing times correspondently longer (on the average 5 minutes).

2. The time of transpiration was kept as short as possible taking into account the sensitivity of the balance. On the average it amounted to 1 minute, but was often shorter or longer depending on the transpiration rate.

3. The heat conduction towards the leaf disc was accelerated by making the leaf holder of a good conducting material (brass) and by putting on the balance scale a small brass pedestal fitting into the leaf holder from below.

The determinations in still air were made in the closed balance case. For those in wind a fan of the type used for hair drying (a so called Föhn), but with the air heating coil switched off, was placed in front of the open door of the balance case with its funnel directed towards the leaf disc at a distance of about 12 cm. The wind velocity over the leaf disc amounted certainly to several meters per second, amply sufficient to blow away all external resistances (cf page 266).

The determinations described above were made with leaf discs upside down and yielded the total (stomatal + cuticular) transpiration rate; the stomatal transpiration rate was obtained by subtracting the cuticular. The latter was determined after the measurement of the stomatal aperture (see below) by inverting the leaf disc in the holder and making a second transpiration measurement in the same way. In so doing one takes for granted that the cuticular transpiration rates of the upper and lower sides of the leaf are equal and that cuticular and stomatal transpiration are not interdependent. These suppositions may be questionable, but we will leave them out of the discussion because of the relatively small values of the cuticular transpiration rates (cf figs 13 and 14)*.

At the beginning of each transpiration measurement the air temperature was read on a thermometer (accurate to 0.5°C) and the air humidity on a Haenni hair hygrometer (accurate to 1 % relative humidity).

C. *Determination of stomatal aperture*

The measurement of stomatal aperture took place immediately after the transpiration measurement of the lower leaf side. The leaf disc was taken out of its holder and put dry on to a slide. It was inspected under the microscope in transmitted light with a magnification of 450 x. The measurements were made by means of a calibrated ocular micrometer, the scale divisions of which corresponded to 3.5μ . Apertures were estimated to 1/10 of a scale division, i.e. to 0.35μ .

As mentioned earlier the stomatal slit in this test plant gives a sharp image against the deep substomatal space below. The measurement was made at the middle of the slit with the microscope focussed at its narrowest part.

There was always considerable variation of stomatal apertures within a leaf, so about 25 measurements were taken at random over the area concerned and the mean calculated from them. These measurements took about 10 minutes. Subsequently, in the same leaf disc two measurements (one on each side of the mid-rib) were made of the number of stomata in the field of vision at a magnification of 55 x, this number varying considerably in different leaves. Again the mean of these two values was calculated and the number N of stomata per cm^2 computed.

An objection against this method might be that during the expe-

* The difference between the cuticular transpiration in still air and in wind is not at all significant.

riment the apertures may change. In that case it would mostly be a closure as the water content of the leaves used is generally suboptimal (STÅLFELT 1929). To check this point the values were grouped as first, second, third etc. measurements. If any general trend had occurred, it would appear from examination of these data. Fig. 12, however, shows no appreciable decline with time, so the conclusion may be drawn that the apertures did not change during the course of the experiment.

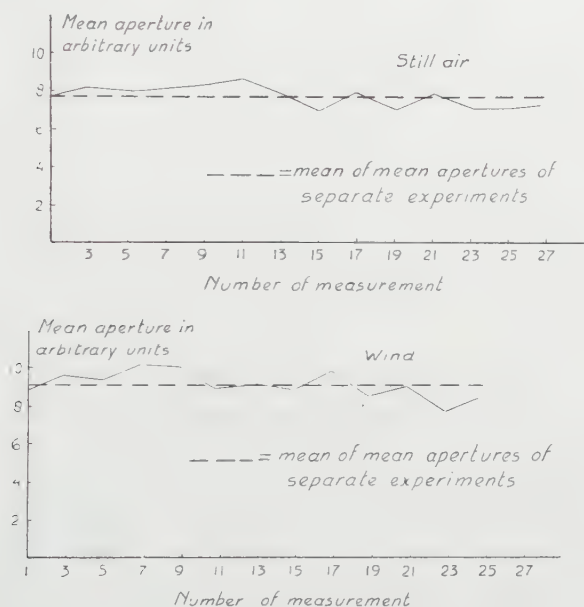


Fig. 12. Mean change of stomatal aperture during a series of 27, resp. 25 measurements.

D. Determination of evaporation in still air

This was done in exactly the same manner as the determination of transpiration, only instead of a leaf disc a disc of wet filter paper was put into the leaf holder. A mean was taken from 14 determinations.

E. Evaluation of the experimental data

As said earlier the water loss from leaf and filter paper discs was expressed in grams per second per cm^2 per % relative humidity deficit. Here the supposition holds that the concentration difference of water vapour $c - c'$ is directly proportional to the external humidity deficit. This means that c , the concentration of water vapour at the walls of the substomatal cavity, is supposed to correspond to the saturated water vapour concentration at the given temperature.

This is not entirely correct since the cells have a certain suction tension or D.P.D. (= diffusion pressure deficit). This D.P.D. tends to lower the water vapour concentration which is in equilibrium with

these cells. However, as GRADMANN (1928) rightly observed, this decrease is very small. Examination of SHULL's (1939) table, which gives the relation between D.P.D. and relative humidity, shows that a D.P.D. value of 13 atm., probably never reached by the leaf cells in our experiments, corresponds to a humidity deficit of only 1 %. Therefore the D.P.D. of the leaf cells could be considered as negligible in comparison with the average humidity deficit of 35 % in our experiments.

To make the data obtained mutually comparable two corrections were still necessary, viz: —

1. for the temperature variations in the experimental room;
2. for the number of stomata per cm² leaf surface.

In the experimental room the temperature varied between 21 and 25° C. All transpiration values were reduced to 23° C by multiplication by the ratio between the saturated water vapour pressure at 23° C and that at the prevailing temperature. This, of course, means a correction for the concentration difference $c - c'$. The diffusion constant k is hardly affected by these temperature differences as it increases proportionally to the square of the absolute temperature only

$$k_2 = k_1 (T_2/T_1)^2.$$

Therefore it was assumed to remain constant.

Also a correction for the number of stomata per cm² leaf area should be applied, but this is possible only if the validity of the principles, which has to be proved, is already taken for granted. Nevertheless these corrections have been applied. In wind the transpiration rate is taken to be directly proportional to the number of stomata per cm². In still air the correction is more difficult to calculate as will be explained in the Appendix (part VI).

Reduction of the transpiration rates to the average number of stomata per cm² leaf surface has the effect of diminishing the spread in the scatter diagrams without essentially changing their position (cf figs 13 and 14). This is what we would expect if our theory is correct.

III. EXPERIMENTAL RESULTS

Figs 13 and 14 show the experimentally determined relation between stomatal aperture and transpiration rate. The spread of the points will be due partly to inaccuracies of the balance since in wind a few negative transpiration rates were found.

The general trend of the curves is in accordance with the theoretical expectations: — in still air a diminishing influence of the stomata with increasing aperture, in wind an approximately linear relation.

However, the curve in wind is certainly not quite linear, being much steeper near its origin (between apertures 0 and 2μ). In STÅLFELT's curves also we observe this steepness at small apertures (cf figs 7 and 9).

Several avenues were explored in a vain attempt to find an explanation of this phenomenon, until the solution was found to lie in

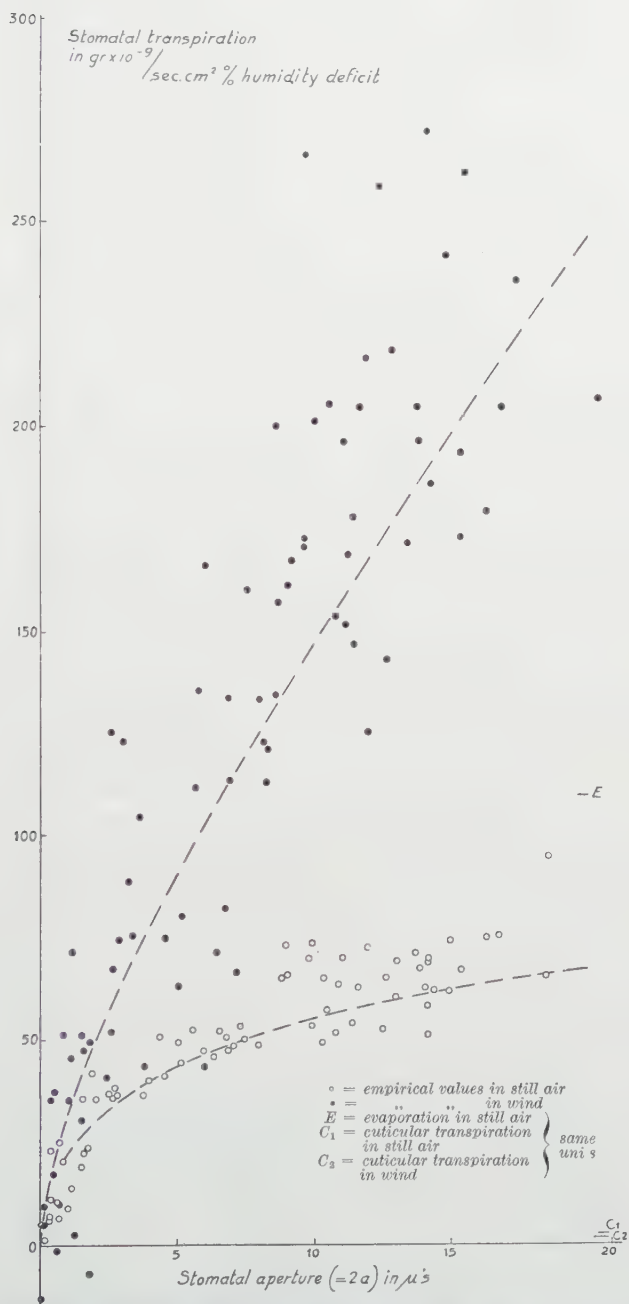


Fig. 13. Relation between stomatal transpiration and aperture in still air and in wind (non-reduced values). The dotted lines represent the corresponding theoretical values.

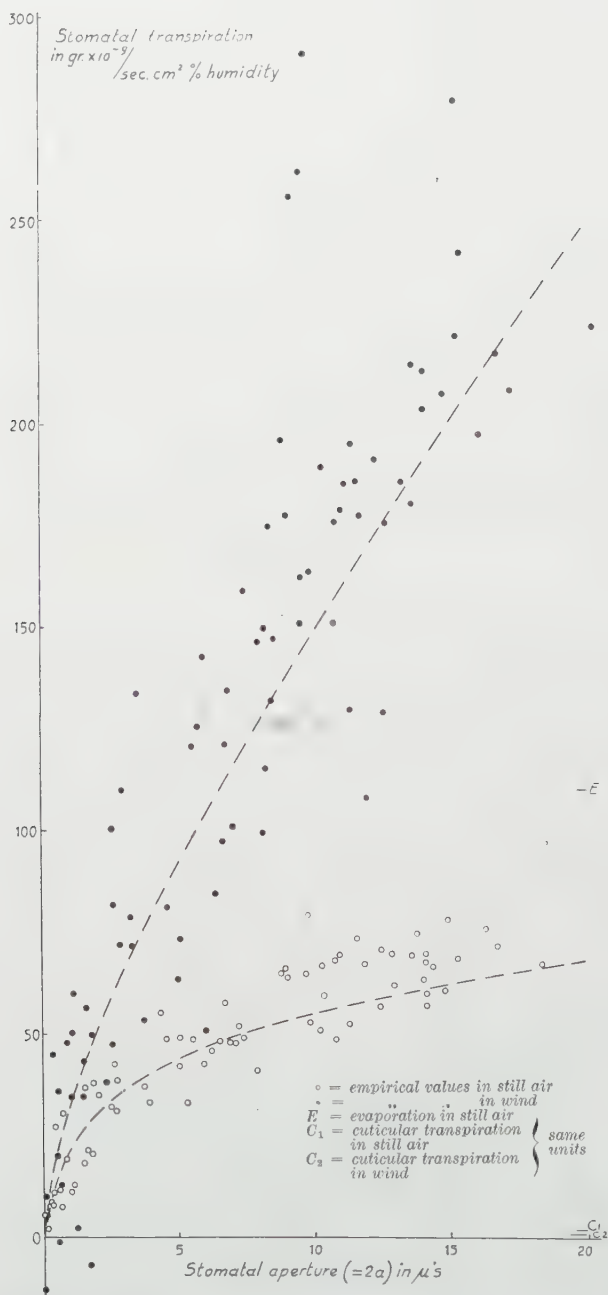


Fig. 14. Relation between stomatal transpiration and aperture in still air and in wind (reduced values). The dotted lines represent the corresponding theoretical values.

the shape of the stomatal pores. In transverse section these pores are hour-glass shaped, i.e. they have a short narrow central part which leads on each side into a long wider part as is shown in fig. 15. This configuration must be responsible for the phenomenon observed on the following grounds:—

Through a slit of small depth (fig. 16A) the diffusion rate will

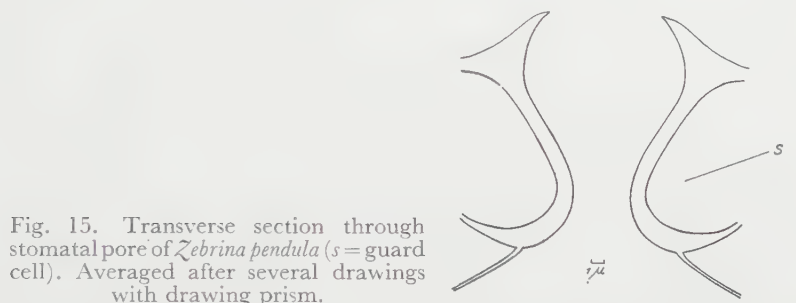
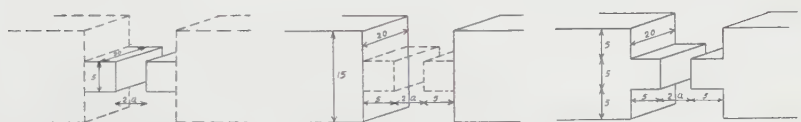


Fig. 15. Transverse section through stomatal pore of *Zebrina pendula* (s = guard cell). Averaged after several drawings with drawing prism.



$$r = \frac{l}{\pi} \frac{s}{2a \times 2c}$$

$$r = \frac{l}{\pi} \frac{1s}{2(a+s) \times 20}$$

$$r = \frac{l}{\pi} \left(\frac{s}{2a \times 20} + \frac{10}{2(a+s) \times 20} \right)$$

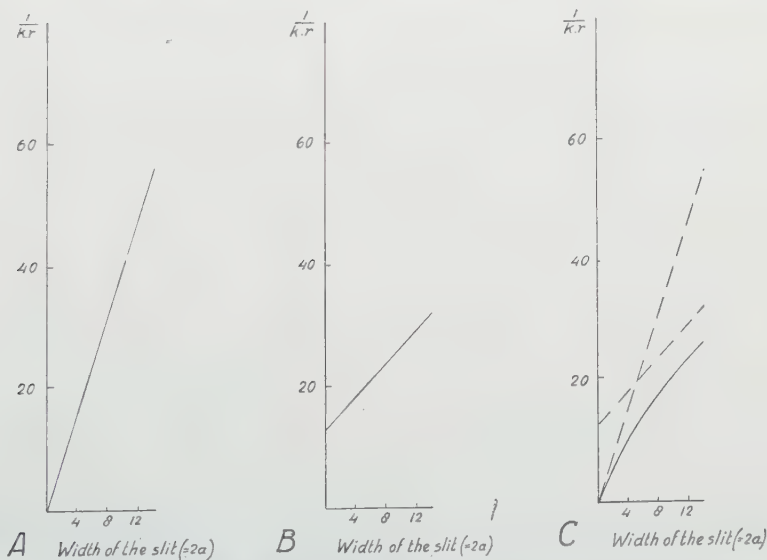


Fig. 16. Scheme of the influence of the configuration of the stomatal pore on the relation between stomatal transpiration and aperture in wind. A. Slit of small depth. B. Slit of great depth. C. Combination of A and B.

increase very rapidly with increasing width resulting in a steep diffusion curve. The corresponding diffusion curve for a deep slit (fig. 16B) will be much less steep. If we now take a combination of the two in such a way that the shallow part projects inward from the deeper part (fig. 16C) the following effect will be obtained. If the slit is nearly closed, it is the shallow part which has the greater resistance of the two and therefore determines the steepness of the diffusion curve. The wider the slit opens the more the curve tends to become parallel to that of the deeper part.

The same reasoning explains why even at microscopically "closed" stomata still a relatively large transpiration ("substomatal transpiration", cf STÅLFELT 1932) can occur.

The question still remained whether the experimental data could be explained quantitatively by means of the principles outlined in the introduction. To decide this point all diffusion resistances had to be calculated as exactly as possible in their relation to the stomatal aperture, viz: —

1. The resistance in the substomatal cavity* which was represented by a spherical space; for mathematical reasons the lower part of the stoma was included in this calculation (fig. 17).

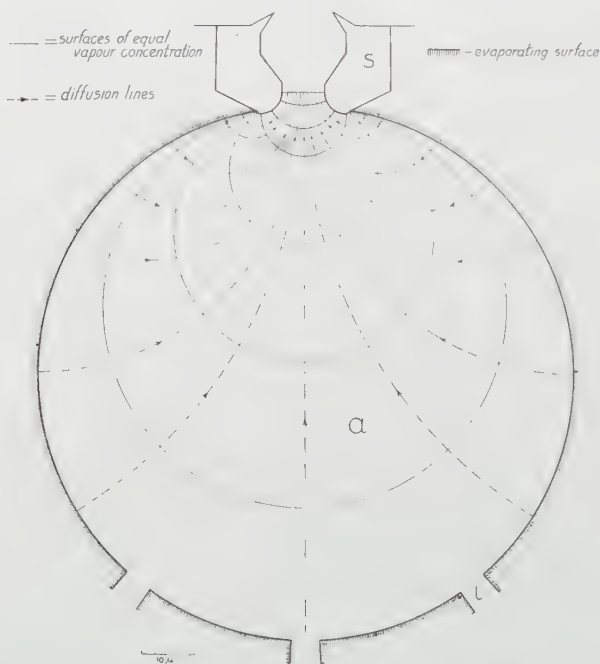
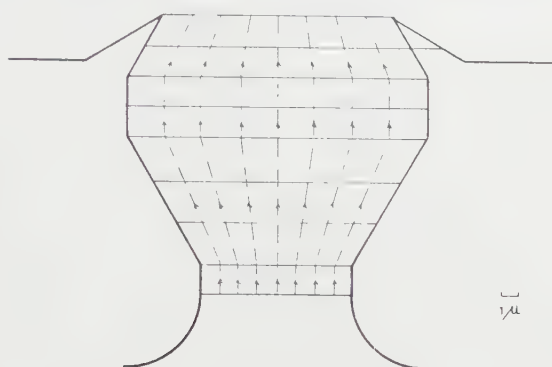


Fig. 17. Schematic representation of the substomatal cavity (a = substomatal cavity, s = stomatal guard cell, i = intercellular space)

* For the sake of simplicity we left out of account this resistance in the introduction and supposed the water vapour concentration in these cavities to be saturated.

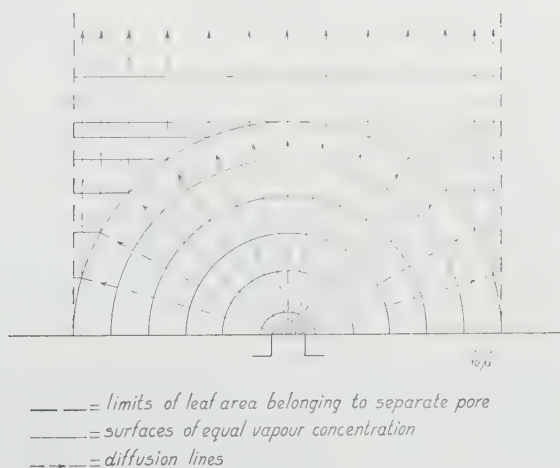
2. The resistance in the remaining part of the stoma (fig. 18); as in calculation 1 the actual shape of the stomata was taken into account as much as possible.



— = *planes of equal vapour concentration*
 - - - - - = *diffusion lines*

Fig. 18. Schematical representation of the stomatal pore.

3. The resistance in the micro vapour cups over the stomata making allowance for their limited size (fig. 19).



— = *limits of leaf area belonging to separate pore*
 — = *surfaces of equal vapour concentration*
 - - - - - = *diffusion lines*

Fig. 19. Schematical representation of a micro vapour cup of limited size.

The corresponding calculations may be found in the Appendix (parts I, II and III).

As mentioned in the introduction the fourth resistance, that of the macro vapour cup, was determined empirically. It appeared to be equivalent to that of a still air layer of a thickness of 0.55 cm.

Fig. 20 shows the relation between these four resistances (calculated

for 1 cm² leaf area with a mean of 1625 stomata) and the stomatal aperture. It is clear that the resistances 1 and 2 which both include the narrowest part of the stoma approach infinity at complete stomatal closure. This is not the case for the third resistance (micro vapour cups) as this begins at the outer part of the stoma which is never completely closed.

In still air the total diffusion resistance was obtained by addition of all four, in wind we assumed (cf page 266) that the two external resistances had been eliminated (fig. 20).

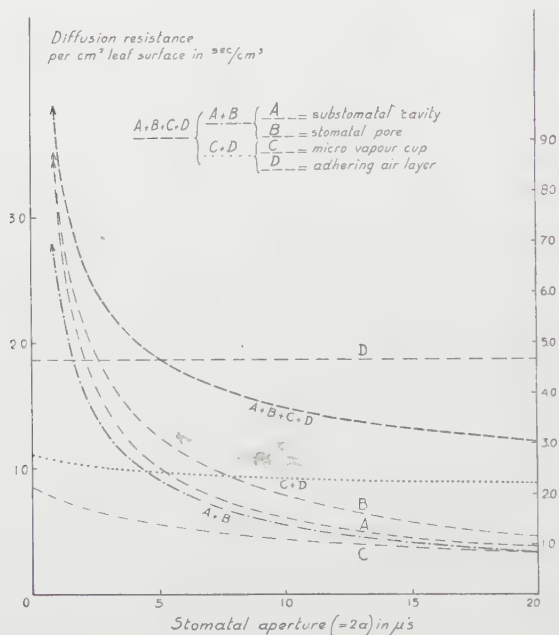


Fig. 20. Theoretical value of the separate and combined diffusion resistances in relation to the stomatal aperture. The ordinate to the left applies to the separate resistances, the ordinate to the right to the combined ones.

Knowledge of the total resistance enables us to calculate the corresponding transpiration rate. This is done by dividing this resistance into the concentration difference $c - c'$ for 1 % saturation deficit.

The curves in figs 13 and 14 are not free-hand curves drawn through the scatter diagrams, but the theoretical curves calculated in the manner described. The agreement between theory and experiment is very good, even though the theoretical curves are somewhat too low. The cause of this discrepancy may be found either in the inevitable errors in making approximations for the shape of the diffusion system or in the choice of the value of the diffusion constant of water vapour in air. According to STEFAN (cf BROWN and ESCOMBE 1900) the theoretical value of this constant at 0° C is 0.229, yielding 0.269 for its value at 23° C (see formula page 272), but the values determined

experimentally deviate from it in both directions. We took SUMMER-HAYE'S (LANDOLT-BÖRNSTEIN 1935) experimental value of 0.282 at 16.1° C from which a value of 0.296 at 23° C was derived. As STEFAN'S theoretical value applies only to completely still air which will hardly ever exist the choice of a somewhat higher experimental value may be justified.

IV. DISCUSSION

The experimental results lead us to the conclusion that in our case stomatal transpiration could be explained quantitatively as an evaporation of water in air through a variable system of successive diffusion resistances. Consequently, under the experimental conditions described, for all apertures, up to the widest encountered, the stomata were the only physiological factor controlling transpiration.

From this it follows that no measurable resistance against water loss was found apart from that in the gaseous phase and that there was no evidence of any influence of incipient drying of cell walls.

This does not prove that incipient drying will never be of any importance. One might argue that in our experiments the time of transpiration was too short to bring about this phenomenon. It is a pity that the experiments of STÅLFELT (1932*a* and *b*) in which the time of transpiration was much longer do not allow an exact theoretical analysis because of lack of data about the temperature of the leaves and evaporimeters.

STÅLFELT himself (1932*a*), however, collected evidence against such an incipient drying by proving that the rate of transpiration was largely independent of the leaf water content. This result was confirmed by GREGORY and co-workers (1950).

Meanwhile, we do not set a great value upon this argument. The D.P.D. values of the leaf cells, even at a water loss of 39 % (STÅLFELT), are not very low in comparison with those of the air (SHULL 1939, cf page 272). It is quite imaginable that incipient drying phenomena, if at all present, only occur at high transpiration rates, when a sufficient D.P.D. gradient through the cell walls lining the intercellular spaces occurs. Therefore, in our view much stronger evidence against an incipient drying of mesophyl cell walls, not mentioned by STÅLFELT, is provided by his statement that the relative transpiration rate at given stomatal aperture is completely independent of the actual evaporation rate which varied in his experiments from 110 to 1000 mg per hour and per 25 cm².

Altogether relating our results to those of others we consider the evidence for an incipient drying regulation of stomatal transpiration rather scarce. Yet we do not deny its theoretical possibility, the more so as it has become probable that all mesophyl cell walls are clothed with a submicroscopic cuticle like layer (FREY-WYSSLING and ELSA HAUSERMANN 1941, cf LEWIS 1948). We are aware that this fact renders the theoretical arguments against incipient drying of RENNER (1915) and VAN DEN HONERT (1948) less conclusive because in them

the supposition prevails that the walls of intercellular spaces are structurally identical with the walls between cells.

Finally it may be stressed that both STÅLFELT and we used hygromorphous test plants, so our conclusion may hold for this ecological type only and not for the meso- or xeromorphous type. This problem must be solved experimentally.

To conclude we may say that there is not sufficient evidence to throw serious doubt on the theory of stomatal control of transpiration.

SUMMARY

The old question, whether the stomata are the only mechanism by which the plants can regulate their transpiration rate or whether other physiological factors beside the stomata play a regulating role, was subjected to an experimental study.

To this purpose experimental transpiration rates in still air as well as in wind were compared to those to be expected theoretically at the same stomatal aperture, if the stomata really are the only factor regulating transpiration. The former were determined by weighing leaf discs of the test plant — *Zebrina pendula* — before and after a short time of transpiration, the latter by calculating in simplified models the successive resistances to water vapour diffusion in the leaf in their relation to the stomatal aperture. The external resistance only, which exists in still air and which is hardly amenable to an exact theoretical analysis, was derived from comparable evaporation experiments. Stomatal apertures were determined by direct measurement under the microscope.

On comparison there appeared to be a close agreement between the experimental and theoretical values.

To test the applicability of the principles used in the calculation an analysis along the same lines of thought was made of the experiments on evaporation through multiperforate septa by SIERP and SEYBOLD (1929) and by HUBER (1930). The agreement with their experimental results was satisfactory.

The conclusion was drawn that under the conditions of the experiments the stomata, up to their maximal aperture, were the only physiological factor controlling transpiration.

APPENDIX

I. CALCULATION OF THE DIFFUSION RESISTANCE IN THE SUBSTOMATAL CAVITY

This calculation will be based on the evaluation of the diffusion resistance in a body which is formed by allowing the thick-lined part of fig. 21 to rotate on its axis of symmetry GF. Only the concave part of the inner wall of this body (indicated by shading) is supposed to

be evaporating. Between the convex bodies it is open at the upper side.

In this body the surfaces of equal vapour concentration are supposed to be parts of spherical surfaces the centres of which lie on the axis of rotation GF and which all pass through the circle drawn by the

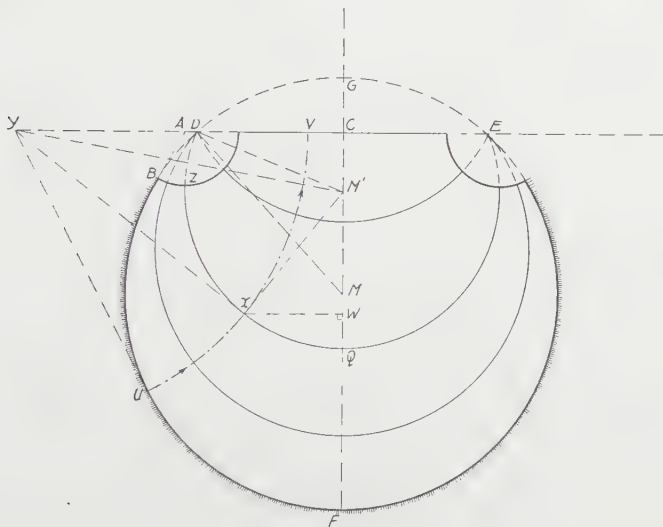


Fig. 21

rotation of point D (E). The corresponding diffusion lines may be constructed as shown in the figure. Their perpendicular relation to the surfaces of equal vapour concentration is apparent from the equality

$$YU^2 = YX^2 = YD \times YE.$$

We are aware that these surfaces do not satisfy the Laplace equation, but they are supposed to be a sufficiently close approximation to the actual conditions (see page 283).

For the sake of brevity we will use the following symbols:—

$AB = a$	$\text{arc } DF = b$	$M'X = s(v)$
$AC = p$	$XY = u$	$XW = w(u, v)$
$DC = q$	$YC = y(u)$	$\text{arc } XV = x(u, v)$
$MF = MD = r$	$M'C = v \text{ or } -v \text{ (according to the situation of } M' \text{ on this side or on the other side of } C)$	$\text{arc } XZ = z(u, v)$

As in this case the surfaces of equal vapour concentration are not flat we must use the following expression of Fick's law

$$i = k \cdot \partial c / \partial x,$$

wherein i = quantity of matter diffusing through unit of area of a surface of equal vapour concentration in unit of time.

This expression is applicable to any point in the body of rotation. We will apply it to point X of an arbitrary surface of equal vapour concentration.

Choosing u and v as independent variables in our calculation we get (on the above assumption)

$$(1) \quad i = k \cdot \frac{\partial c}{\partial x} = k \cdot \frac{dc}{dv} \cdot \frac{\partial v}{\partial x}.$$

Now we have

$$x = u \cdot \text{angle VYX (in radians)}$$

and

$$\sin \text{VYX} = \sin (\text{VYM}' + \text{M}'\text{YX}) = \frac{uv + ys}{u^2 + s^2} = S \text{ (say),}$$

whence

$$x = u \cdot \sin^{-1} S \quad (\text{if angle VYX} < \pi/2)$$

$$\text{or} \quad x = u(\pi - \sin^{-1} S) \quad (\text{if angle VYX} > \pi/2).$$

We are now able to compute how x changes in relation to v , as

$$\begin{aligned} \frac{\partial x}{\partial v} &= \frac{\partial x}{\partial S} \cdot \frac{\partial S}{\partial v} = \frac{u}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial v} \quad (\text{if angle VYX} < \pi/2) \\ \text{or} &= \frac{-u}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial v} \quad (\text{if angle VYX} > \pi/2) \\ &= \frac{u}{s} \cdot \frac{(u^2 - s^2)(us + yv) + 2usq^2}{(u^2 + s^2)(uy - vs)} \quad (\text{in either case}) \\ &= \frac{u}{s} \cdot T \quad (\text{say}). \end{aligned}$$

Substitution in equation (1) yields

$$(1a) \quad i = k \cdot \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv}.$$

If now we introduce the quantity J = quantity of matter diffusing through a surface of equal vapour concentration in unit of time, we have

$$(2) \quad J = \int i \cdot dO = k \cdot \int \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv} \cdot dO.$$

In this expression dO represents the area described by the element of area in the point X when rotating on the axis of symmetry GF. In this rotation the point X describes a circle with radius w (u, v).

We can compute dO as a function of u and v in the following way. We have

$$dO = dz \cdot 2\pi w = dz \cdot 2\pi s \cdot \sin \text{VYX} = dz \cdot 2\pi s \cdot \frac{uv + ys}{u^2 + s^2}.$$

As the quantity O is considered to be defined on the surfaces on which v is constant, the changes of z in relation to u only are of interest. Since

$$z = \text{arc } ZQ - \text{arc } XQ = \text{arc } ZQ - s \cdot \text{angle } VYX,$$

z changes in relation to u according

$$\frac{\partial z}{\partial u} = \partial \left(-s \cdot \sin^{-1} \frac{uv+ys}{u^2+s^2} \right) / \partial u \quad (\text{if angle } VYX < \pi/2)$$

$$\text{or} = \partial \left(-\pi s + s \cdot \sin^{-1} \frac{uv+ys}{u^2+s^2} \right) / \partial u \quad (\text{if angle } VYX > \pi/2)$$

$$= \partial \left(\pm s \cdot \sin^{-1} S \right) / \partial u$$

$$- \frac{\partial z}{\partial S} \cdot \frac{\partial S}{\partial u} = \frac{\pm s}{\sqrt{1-S^2}} \cdot \frac{\partial S}{\partial u}$$

$$= \frac{s}{y} \cdot \frac{(u^2-s^2)(us+yv)+2usq^2}{(u^2+s^2)(uy-vs)} \quad (\text{in either case})$$

$$= \frac{s}{y} \cdot T.$$

Consequently

$$dO = T \cdot \frac{s}{y} \cdot 2\pi s \cdot \frac{uv+ys}{u^2+s^2} \cdot du.$$

Substitution in equation (2) yields

$$J = k \cdot \int \frac{s}{u} \cdot \frac{1}{T} \cdot \frac{dc}{dv} \cdot T \cdot \frac{s}{y} \cdot 2\pi s \cdot \frac{uv+ys}{u^2+s^2} \cdot du$$

$$(2a) \quad = 2\pi k \cdot \int \frac{s^3}{uy} \cdot \frac{uv+ys}{u^2+s^2} \cdot \frac{dc}{dv} \cdot du.$$

Denoting

$$\frac{s^3}{uy} \cdot \frac{uv+ys}{u^2+s^2}$$

by $f(u,v)$ for convenience' sake this expression runs

$$(2b) \quad J = 2\pi k \cdot \int f(u,v) \cdot dc/dv \cdot du.$$

It can be demonstrated* that if the spherical surfaces considered should be such that one function c exists depending on v only and satisfying the Laplace equation, then $f(u,v)$ can be written as $m(u)/n(v)$ and c satisfies the equation

$$dc/dv = \kappa \cdot n(v).$$

In this case equation (2b) passes into

$$J = 2\pi k \cdot \int \frac{m(u)}{n(v)} \cdot \kappa \cdot n(v) \cdot du$$

$$= 2\pi k \cdot \kappa \cdot \int m(u) \cdot du,$$

whereas

$$(c-c') = \kappa \cdot \int n(v) \cdot dv.$$

* The author owes the arguments printed in small type to Dr H. R. VAN DER VAART who was kind enough to test the relationship between our surfaces and the Laplace equation.

So

$$(3) \quad \frac{c-c'}{J} = R = \frac{\int n(v) \cdot dv}{2\pi k \cdot \int n(u) \cdot du}.$$

However this condition is not complied with. Accordingly the function $f(u, v)$ can not be split up into a function of u and a function of v . So the method used in the following is not correct from a mathematical point of view, but approximate. If the condition described is satisfied, equation (3a) resulting from this method (see below) reduces to equation (3), as one can easily see by replacing $f(u, v)$ in (3a) by $m(u)/n(v)$.

Differentiating (2b) with respect to u we find

$$\frac{dJ}{du} = 2\pi k \cdot f(u, v) \cdot \frac{dc}{dv}$$

or

$$\frac{dc}{dv} = \frac{1}{2\pi k} \cdot \frac{1}{f(u, v)} \cdot \frac{dJ}{du}.$$

Acting as if dJ/du did not depend on v we find on integration

$$c-c' = \frac{1}{2\pi k} \cdot \frac{dJ}{du} \cdot \int_{-\infty}^{\sqrt{r^2-q^2}} \frac{dv}{f(u, v)},$$

whence

$$\frac{dJ}{du} = 2\pi k \cdot \frac{c-c'}{\int_{-\infty}^{\sqrt{r^2-q^2}} \frac{dv}{f(u, v)}}.$$

If $c-c'$ were independent of u it would follow that

$$J = 2\pi k \cdot (c-c') \cdot \int_a^{+\infty} \frac{du}{\sqrt{r^2-q^2}} \int_{-\infty}^{\sqrt{r^2-q^2}} \frac{dv}{f(u, v)}$$

and that

$$(3a) \quad R = \frac{c-c'}{J} = \frac{(2\pi k)^{-1}}{\int_a^{+\infty} \frac{du}{\sqrt{r^2-q^2}} \int_{-\infty}^{\sqrt{r^2-q^2}} \frac{dv}{f(u, v)}}.$$

Now we use this expression as an approximation to R supposing that $f(u, v)$ can be approximated closely enough by a quotient $m(u)/n(v)$.

As

$$\int_{-\infty}^{\sqrt{r^2-q^2}} \frac{uy}{s^3} \cdot \frac{u^2+s^2}{uv+ys} \cdot dv = \frac{uy^2 \cdot \text{angle FMD}}{q^3} + \frac{u^2y}{sq^2}$$

and

$$\int_a^{\infty} \frac{sq^3}{suy^2 \cdot \text{angle FMD} + qyu^2} \cdot du = \frac{q}{\text{angle FMD}} \cdot \log_e \frac{pb+aq}{ab+aq}$$

the value of R becomes

$$(4) \quad R = \frac{\text{angle FMD}}{2\pi k \cdot q \cdot \log_e \frac{pb+aq}{ab+aq}}.$$

If v varies between finite values, e.g. from $\sqrt{r^2 - q^2}$ to $\sqrt{r'^2 - q^2}$ the expression for the diffusion resistance becomes, as will be easily seen

$$(5) \quad R' = \frac{\text{angle MDM}'}{2\pi k \cdot q \cdot \log_e \frac{rr'p \cdot \text{angle MDM}' + (r'-r)qa}{rr'a \cdot \text{angle MDM}' + (r'-r)qa}}.$$

Now in order to realize as close an approximation as possible to the actual form of the substomatal cavity (cf fig. 10) two of such systems (fig. 22) were connected in series, the lowest part of the stomatal slit being included in one of them. The measurements indicated in the figure have been adapted as well as possible to the actual values.

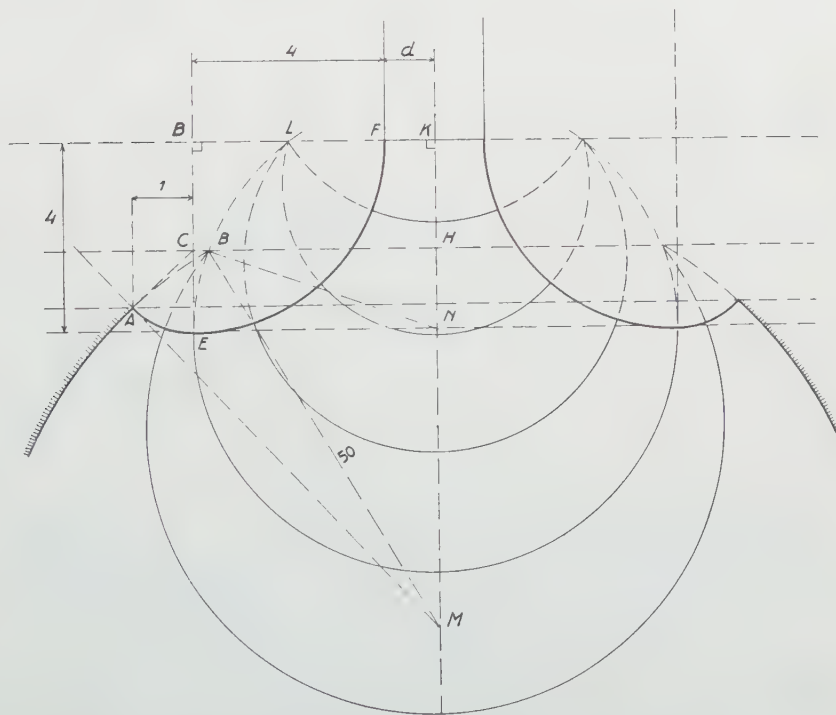


Fig. 22

Computation of the diffusion resistance in these systems proceeds as follows.

System I

The appropriate formula for this system is (5) because v varies between finite values (from MH to NH). Thus we have

$$R_I = \frac{\text{angle MBN}}{2\pi k \cdot \text{BH} \cdot \log_e \frac{\text{BM} \cdot \text{BN} \cdot \text{angle MBN} \cdot \text{CH} + (\text{BN} - \text{BM}) \cdot \text{BH} \cdot \text{AC}}{\text{BM} \cdot \text{BN} \cdot \text{angle MBN} \cdot \text{AC} + (\text{BN} - \text{BM}) \cdot \text{BH} \cdot \text{AC}}}$$

Let d be the radius of a circle the area of which equals the area of the stomatal slit in the narrowest part ($\pi d^2 = \pi \cdot \text{half long axis} \cdot \text{half short axis of the ellipse}$), then we have

$$\text{BM} = 50, \text{BN} = \text{EN} = \text{CH} = d+4, \text{AC} = \frac{50}{\sqrt{50^2 - (d+5)^2}},$$

$$\text{BH} = \sqrt{(d+4)^2 - \text{AC}^2} \quad (\text{as HN} = \text{CE} = \text{AC})$$

$$\text{and} \quad \text{angle MBN} = \text{angle (MBH} - \text{HBN)} = \sin^{-1} z,$$

$$\text{wherein} \quad z = \frac{\text{BH}(\sqrt{50^2 - \text{BH}^2} - \text{HN})}{50(d+4)}.$$

As d is the only variable in each expression R_I can be computed for various stomatal apertures.

System II

The appropriate formula for this system is (4) because v varies from NK to $-\infty$. Thus we have

$$R_{II} = \frac{\text{angle LNT}}{2\pi k \cdot \text{LK} \cdot \log_e \frac{\text{GK} \cdot \text{arc LT} + \text{GE} \cdot \text{LK}}{\text{GE} \cdot \text{arc LT} + \text{GE} \cdot \text{LK}}}$$

Expressing again the various quantities in this equation as functions of d we get

$$\text{LK} = \sqrt{d^2 + 8d}, \text{GK} = d+4, \text{arc LT} = (d+4) \cdot \text{angle LNT}$$

$$\text{and} \quad \text{angle LNT} = \cos^{-1} \frac{-4}{d+4}.$$

So R_{II} can be calculated as a function of d .

Addition of R_I and R_{II} yields the total resistance of the substomatal cavity (including the lowest part of the stoma) and hence this resistance can be calculated for various stomatal apertures (see fig. 20).

II. CALCULATION OF THE DIFFUSION RESISTANCE IN THE STOMA

The schematic representation of the stomatal slit which we used in this calculation is shown in fig. 23. Four systems can be distinguished

indicated in the figure as III, IV, V and VI, the undermost part of the slit having been included in the substomatal cavity. The measurements approximate as closely as possible to the actual values.

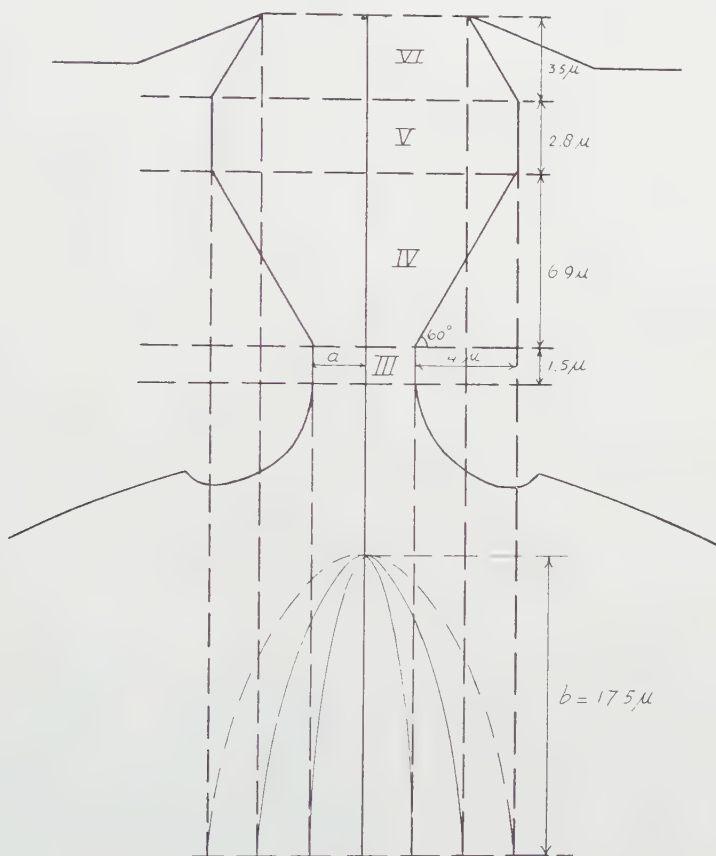


Fig. 23

System III

Here we have

$$R_{\text{III}} = \frac{1}{k} \cdot \frac{h_3}{\pi a b} = \frac{1}{k} \cdot \frac{1.5}{3.14 \times 17.5 \times a}.$$

System IV

In estimating the resistance in this system (fig. 24) we may proceed in the following way.

As an approximation let us suppose that c depends on h only (h represents the length of the perpendicular to the basal plane) and so the surfaces of equal vapour concentration to be flat and perpendicular to the axis of the stomatal slit, then we can write

$$i = -k \cdot \pi a_h b \cdot dc/dh$$

or

$$dc = \frac{-i}{k \cdot \pi b} \cdot \frac{dh}{a_h} = \frac{-i}{k \cdot \pi b} \cdot \frac{dh}{a + h \cdot \cot \alpha}.$$

Integration of c with respect to h (h varying from 0 to $(a' - a) \cdot \tan \alpha$) yields

$$c - c' = \frac{-i}{k \cdot \pi b} \int_{(a' - a) \cdot \tan \alpha}^0 \frac{dh}{a + h \cdot \cot \alpha} \\ = \frac{i \cdot \log_e(a'/a)}{k \cdot \pi b \cdot \cot \alpha}.$$

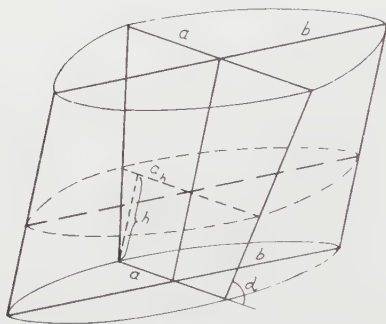


Fig. 24

Thus the diffusion resistance in this system amounts to

$$R_{IV} = \frac{\log_e(a'/a)}{k \cdot \pi b \cdot \cot \alpha} = \frac{\log_e(a+4)/a}{k \times 3.14 \times 17.5 \times 0.58}.$$

Some loss of accuracy results from the use of the approximation for the shape of the surfaces of equal vapour concentration. The extent of this depends on the size of angle α and as in this case its minimal value is 60° deviations will not be large.

System V

Here we have

$$R_V = \frac{1}{k} \cdot \frac{h_5}{\pi(a+4)b} = \frac{1}{k} \cdot \frac{2.8}{3.14 \times 17.5 \times (a+4)}.$$

System VI

Applying to this system the same formula as was developed for system IV we find

$$R_{VI} = \frac{\log_e(a'/a'')}{k \cdot \pi b \cdot \cot \alpha} = \frac{\log_e(a+4)/(a+2)}{k \times 3.14 \times 17.5 \times 0.58}.$$

The algebraical sum of these four resistances gives the total resistance in the stoma for a given value of a (see fig. 20).

III. CALCULATION OF THE DIFFUSION RESISTANCE WITHIN A VAPOUR SHELL OF LIMITED SIZE

The shape of the surfaces of equal vapour concentration extending over a perforated septum will be very complicated from a mathematical point of view. As an approximation we used the schematical representation shown in fig. 19.

The formula of BROWN and ESCOMBE for the resistance of a vapour shell (cf page 258) must be adapted to meet the special case where the size is limited. The following method may be used.

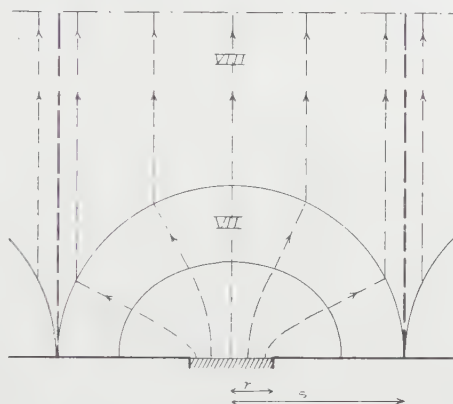


Fig. 25

Surfaces of equal vapour concentration (fig. 25) at a distance of say $5r$ from the evaporating surface (r = radius of this surface) may be regarded as spherical which implies the equality of the vapour concentration gradient at all points of these surfaces. Thus we have

$$i = -k \cdot O \cdot dc/ds = -k \cdot 2\pi s^2 \cdot dc/ds$$

(s = radius of the surface considered).

Integration of c with respect to s (s varying from s' to $+\infty$) gives the fall in vapour concentration and thus the resistance between this surface and the surface at infinity

$$c = \frac{-i}{k \cdot 2\pi} \int_{+\infty}^{s'} \frac{ds}{s^2} = \frac{1}{k} \cdot \frac{i}{2\pi s'}$$

therefore

$$R' = \frac{1}{k} \cdot \frac{1}{2\pi s'}$$

Reducing the resistance in the vapour shell of unlimited size by this amount we get the resistance in the shell of limited size (system VII)

$$R_{VII} = \frac{1}{k} \cdot \left(\frac{1}{4r} - \frac{1}{2\pi s'} \right).$$

The actual value of s' depends on N = number of pores (stomata) per cm^2 according

$$\pi s'^2 = 1/N$$

and the quantity r is related to a by the equation

$$\pi r^2 = \pi(a+2)b = 3.14 \times 17.5 \times (a+2),$$

r being the radius of a circle the area of which equals the area of the stomatal opening at the end of the slit.

Here the supposition prevailed that the formula for the vapour shell resistance over a circular evaporating surface equally holds for an elliptical surface of the same area. According to STEFAN (1881) deviations will not be large as long as the eccentricity of the ellipse is small. At narrow stomatal slits this requirement is not complied with, but in this case the resistance in the shells is only a small fraction of the total resistance, so the inaccuracy introduced will be negligible.

Further it might be questioned whether the thickness of the still air layer (system VIII) should not be reduced by $2/3$ of the height (s') of the vapour shells. In our experiments, however, this correction could be omitted on account of its smallness ($\pm 2.5\%$).

The value of the resistance in the micro vapour cups at various stomatal apertures is given in fig. 20.

IV. THEORETICAL ANALYSIS OF THE EXPERIMENTS ON MODELS BY SIERP AND SEYBOLD (1929)

In the experiments which they made on the evaporation through multiperforate septa SIERP & SEYBOLD used brass boxes covered by perforated thin brass sheets. The diameter of these boxes amounted to 45 mm, their height to 21 mm and the thickness of the brass sheets to 20μ . These sheets had a perforated area of 20×20 mm. The total area of the pores was constant (3.14 mm^2), but the radius of the pores varied from 1000μ to 5μ (boxes I—V). Another box (Q_4) had a cover without pores, but with a square opening of 20×20 mm.

These boxes were filled with water up to 7 mm below the cover and allowed to evaporate under a bell-glass under which P_2O_5 (at the bottom) maintained a constant gradient of vapour concentration. The evaporation power of a box was measured by its decrease in weight after a given time.

Fig. 4 shows the results obtained by the authors (drawn from table 3, page 249), the abscissa representing the diameter of the pores, the ordinate the evaporation power of the box in question in relative units. The evaporation power of the additional box Q_4 is taken as 1.0.

The authors tested the theoretical analysis of these results based on the formulae of BROWN & ESCOMBE and their interpretation was that the theoretical and the experimental data did not agree. From this they concluded that these formulae had no practical value especially for pores of stomatal size.

This conclusion appears to be unfounded. The authors took the evaporation power of the box containing the largest pores as a unit of reference and expressed the other ones in terms of it. However, the greatest deviations are to be expected from the largest pores as in this case the macro vapour cup and the micro ones can no longer be treated as separate systems. So this lack of agreement is not surprising.

How closely indeed the actual and calculated values can agree will be shown for some of their experiments.

When no filter paper was used four diffusion resistances were placed between the evaporating surface and the free (i.e. circulating) air, viz :—
1. The resistance between the evaporating surface (area = $\pi \times 2.25^2 = 16 \text{ cm}^2$) and the perforated part of the brass sheet (area = 4 cm^2).

Simplifying matters by taking an average value of $\sqrt{4 \times 16} = 8 \text{ cm}^2$ for the area of the cross section of this part we compute the following resistance

$$R_1 = \frac{1}{k} \cdot \frac{0.7}{8} = \frac{0.088}{k}.$$

2. The resistance in the pores which had the constant value of

$$R_2 = \frac{1}{k} \cdot \frac{0.002}{0.0314} = \frac{0.064}{k}.$$

3. The resistance in the micro vapour shells under and over each pore. We will leave out of account the limited size of these shells because of their relatively great mutual distance. Doing so we compute their resistance as

$$R_3 = \frac{1}{k} \cdot \frac{1}{N} \cdot \frac{1}{2r}$$

(N = total number of pores in the sheet,
 r = radius of pores).

From this formula we get the following values of this resistance for the several boxes:—

Box I	($N = 1, r = 1 \text{ mm}$)	$R_3 = k^{-1} \cdot 5$
Box II	($N = 400, r = 0.05 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.25$
Box III	($N = 1600, r = 0.025 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.125$
Box IV	($N = 10000, r = 0.010 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.05$
Box V	($N = 40000, r = 0.005 \text{ mm}$)	$R_3 = k^{-1} \cdot 0.025$

4. The resistance in the macro vapour shell (still air layer) extending over the whole perforated area.

As conditions of still air will have been realized very closely under the bell-glass use of BROWN & ESCOMBE's formula seems to be justified

$$R_4 = \frac{1}{k} \cdot \frac{1}{4s} = \frac{1}{k} \cdot \frac{\sqrt{3.14}}{8} = \frac{0.221}{k}$$

(s = radius of circle the area of which equals the area of the perforated part of the sheet).

The diffusion resistance of the additional box Q_4 consists of the resistances R_1 and R_4 only.

Now taking the evaporation power of box Q_4 as a unit we can compute the evaporation power of the other boxes (I—V) by the formula

$$E = \frac{R_1 + R_4}{R_1 + R_2 + R_3 + R_4}.$$

Thus we find the following values

Box I	$E = 0.06^*$
Box II	$E = 0.50$
Box III	$E = 0.62$
Box IV	$E = 0.73$
Box V	$E = 0.78$

In fig. 4A these results are compared with the experimental data (taken from table 3, page 249). The agreement appears to be rather close.

Computing the ratio Q_4/IV and Q_4/V we find 1.37 and 1.28 respectively, whereas the authors record

$Q_4/IV = 1.29$ (table 3, page 249) and 1.39 (mean value from tables 5—8),

$Q_4/V = 1.32$ (table 3, page 249) and 1.20 (table 8, page 252).

Similarly calculating the ratio between the evaporation power of box Q_1 (square opening 1×1 cm) and box IVa (same number and size of pores as box IV, but on an area of 1×1 cm) we get 1.18, whereas SIERP & SEYBOLD actually found a ratio of 1.26 (table 3, page 249) and 1.20 (page 253). The theoretical values of the ratios Q_4/Q_1 and IV/IVa are somewhat lower (11% and 22% respectively) than the experimental ones (table 3, page 249).

When wet filter paper was attached to the lower side of the septum three resistances only are to be taken into account, viz:—

1. The resistance in the pores (R_2) which has the same value as in the first case.
2. The resistance in the micro vapour shells (R_3). As these shells are now present at the upper side of the pores only this resistance amounts to half the value it had in the first case.
3. The resistance in the macro vapour shell (R_4) having again the same value as above.

The diffusion resistance of box Q_4 now consists of resistance R_4 only.

Consequently the relative evaporation power of boxes I—V is given by the formula

$$E = \frac{R_4}{R_2 + R_3 + R_4}.$$

* Strictly speaking our formula for E is less correct for these large pores (cf page 291), so not too great a value should be set on this number.

Thus we find

Box I	$E = 0.08^*$
Box II	$E = 0.54$
Box III	$E = 0.64$
Box IV	$E = 0.71$
Box V	$E = 0.74$

In fig. 4B these results are compared again with the experimental data (taken from table 11, page 255). The agreement is very close indeed.

Comparison of the theoretical and experimental values of the ratios Q_1/IVa , Q_4/Q_1 and IV/IVa yields in this case

	theoretical value	experimental value (table 11, page 255)
Q_1/IVa	1.20	1.29
Q_4/Q_1	2.00	2.20
IV/IVa	1.71	2.08

In the main the lack of agreement between theory and experiment is considered to be much too small to justify the authors' doubt about the practical value of BROWN & ESCOMBE's principles for pores of stomatal size.

V. THEORETICAL ANALYSIS OF THE EXPERIMENTS ON MODELS BY HUBER (1930)

HUBER attacked the problem of evaporation through perforated septa by studying the influence of pore number at constant pore size on the one hand and of pore size at constant pore area on the other. For that purpose he used the following perforated metal sheets (see table I).

The evaporating surface consisted of wet filter paper attached to the lower part of the septum. Evaporation took place into the free air of a room.

TABLE I
Perforated septa used by HUBER

Pore size (= O)	Diameter of pores (= $2r$)	Number of pores (= N)	Perfo- rated area (= P)	Relative area of pores (= A)	Thickness of septum (= d)
1 cm ²	11.3 mm	1-4-9-16-25-36- 49-64	100 cm ²	0.01-0.04-0.09- 0.16-0.25-0.36- 0.49-0.64	0.6 mm
1 mm ²	1.13 mm	25-100-400-625- 1090-1600-2500	100 cm ²	0.0025-0.01-0.04- 0.0625-0.109- 0.16-0.25	0.13 mm
2000 μ^2	50 μ	400-3600-6400- 10000	4 cm ²	0.002-0.018- 0.032-0.05	0.02 mm
80 μ^2	10 μ	2500	1 cm ²	0.002	0.02 mm

* See note on page 292.

Relative evaporation rates were determined using as a base of reference the evaporation power of a septum with a central opening of the same area as the perforated part of the septum in question.

The results are shown in fig. 6 the abscissa representing the relative pore area, the ordinate the relative evaporation power.

The question arises as to whether these results can be explained quantitatively on the principle of consecutive resistances.

Three diffusion resistances are to be taken into account, viz:—

1. The resistance in the pores amounting to

$$R_1 = \frac{1}{k} \cdot \frac{d}{N \cdot O}.$$

2. The resistance in the micro vapour shells. Using the formula for shells of limited size we get

$$\begin{aligned} R_2 &= \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{1}{2\pi s} \right) = \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{1}{2\pi \sqrt{P/\pi N}} \right) \\ &= \frac{1}{k} \cdot \frac{1}{N} \left(\frac{1}{4r} - \frac{\sqrt{A}}{2\pi r} \right). \end{aligned}$$

3. The resistance in the macro vapour shell (still air layer) extending over the whole perforated area. As in the free air of a room conditions of still air will not be realized sufficiently to justify the use of BROWN & ESCOMBE's formula we must write

$$R_3 = \frac{1}{k} \cdot \frac{a}{P}$$

(a = thickness of hypothetical still air layer).

Thus the total resistance is computed as

$$\begin{aligned} R_t &= R_1 + R_2 + R_3 \\ &= \frac{1}{k} \cdot \left(\frac{d}{N \cdot O} + \frac{1}{4r \cdot N} - \frac{\sqrt{A}}{2\pi r \cdot N} + \frac{a}{P} \right) \\ &= \frac{1}{k} \cdot \left(\frac{d}{A \cdot P} + \frac{\pi r}{4A \cdot P} - \frac{r\sqrt{A}}{2A \cdot P} + \frac{a \cdot A}{A \cdot P} \right) \\ &= \frac{1}{k} \cdot \frac{1}{4A \cdot P} (4d + \pi r - 2r\sqrt{A} + 4a \cdot A). \end{aligned}$$

Leaving out of account the thickness of the septum we compute the resistance of the reference septa as

$$R_r = \frac{1}{k} \cdot \frac{a}{P}.$$

So the relative evaporation rates are given by the formula

$$\begin{aligned} E_{\text{rel}} &= \frac{a/P}{(4d + \pi r - 2r\sqrt{A} + 4a \cdot A)/4A \cdot P} \\ &= \frac{4a \cdot A}{4d + \pi r - 2r\sqrt{A} + 4a \cdot A}. \end{aligned}$$

All quantities in this formula are known with the exception of a . The drawback is that this quantity a can be computed only from the experimental data themselves. However, the result of this computation can be made plausible on grounds to be discussed.

The experimental relative evaporation rates of the sheets indicated in italics of table I were substituted in the formula for E_{rel} to calculate a . Thus we found $a = 1$ cm for the sheet with a perforated area of 100 cm^2 ($O = 1 \text{ mm}^2$) and $a = 0.3$ cm for the sheet with a perforated area of 4 cm^2 ($O = 2000 \mu^2$).

The resistances in the adhering air layer then become $0.01/\text{k}$ ($1 \text{ mm}^2\text{-septum}$) and $0.075/\text{k}$ ($2000 \mu^2\text{-septum}$). According to STEFAN's diameter law in perfectly still air the ratio between these resistances would be 1 to 5, whereas in strong wind their ratio would approach to 1 to 25, so it may be seen that the ratio 1 to 7.5 is not unlikely for the prevailing conditions.

The relative evaporation power of the $1 \text{ mm}^2\text{—}$ and $2000 \mu^2\text{—}$ septa at varying pore number and consequently varying pore area as calculated with the aid of the mentioned values of a have been plotted graphically in fig. 6 (dotted lines). Because our formula is not valid for the largest pores as in this case the macro vapour shell and the micro ones can no longer be treated as separate systems, the $1 \text{ cm}^2\text{-septum}$ were not included in the calculation.

There appears to be a very close agreement between the shape of the theoretical and experimental curves, though there are some numerical differences.

The large value (0.6) HUBER found for the relative evaporation rate of the $10 \mu\text{-septum}$ can not be accounted for unless we assume the adhering air layer to be of an unpalusible thickness. Possibly interfering effects (capillary attraction of water by the pores?) are responsible for the discrepancy.

VI. CALCULATION OF THE CORRECTION FOR THE NUMBER OF STOMATA PER cm^2

In still air only a fraction of the total diffusion resistance is inversely proportional to the number of stomata per cm^2 , viz the sum of the resistances of the substomatal cavity, of the stomata and of the micro vapour shells.

Putting this sum (computed for $N = 1625$ — the average number of stomata per cm^2 in our experiments and for a given stomatal aperture) $= R_v$ and putting the resistance in the still air layer per $\text{cm}^2 = R_e$ we have

$$R_t = R_v + R_e$$

wherein R_t = total resistance per cm^2 for $N = 1625$ and for the aperture concerned.

For a leaf with N' stomata per cm^2 the total resistance per cm^2 for the same stomatal aperture becomes

$$R'_t = (1625/N') \cdot R_v + R_e.$$

Consequently

$$\frac{R'_t}{R_t} = \frac{(1625/N') \cdot R_v + R_c}{R_t} - \frac{T}{T'}$$

wherein T = transpiration rate reduced to $N = 1625$ and T' = empirical transpiration rate for N' stomata per cm^2 .

$$\text{Thus} \quad T = T' \cdot \frac{(1625/N') \cdot R_v + R_c}{R_t}$$

The value of R_v , R_c and R_t can be read from fig. 20 for any stomatal aperture, so T can be computed.

ACKNOWLEDGEMENT

The author is greatly indebted to Miss H. Ferres for her corrections in the English text.

REFERENCES

- BACHMANN, F. 1932. Gedanken zur Transpirationsanalyse. *Planta* 16 : 526.
 BREWIG, A. 1933. Ein Beitrag zur Analyse des Transpirationswiderstandes. *Planta* 20 : 734.
 BROWN, H. & F. ESCOMBE. 1900. Static diffusion of gases and liquids in relation to the assimilation of carbon and translocation in plants. *Phil. Trans. Roy. Soc. London, Ser. B*, 193 : 223.
 DARWIN, Fr. 1916. On the relation between transpiration and stomatal aperture. *Phil. Trans. Roy. Soc. London, Ser. B*, 207 : 413.
 FIRBAS, F. 1931. Die Wirkung des Windes auf die Transpiration. *Ber. dtsch. bot. Ges.* 49 : 443.
 FREY-WYSSLING, A. & ELSA HAUSERMANN. 1941. Ueber die Auskleidung der Mesophyllinterzellularen. *Ber. schweiz. bot. Ges.* 51 : 430.
 FUESSER, K. 1933. Die Transpiration und die Transpirationswiderstände verschiedener Pflanzentypen. *Planta* 19 : 465.
 GÄUMANN, E. & O. JAAG. 1938. Untersuchungen über die stomatäre Transpiration. *Ber. schweiz. bot. Ges.* 48 : 45.
 GÄUMANN, E. & O. JAAG. 1939a. Der Einfluss des Windes auf die pflanzliche Transpiration I. *Ber. schweiz. bot. Ges.* 49 : 178.
 GÄUMANN, E. & O. JAAG. 1939b. Der Einfluss des Windes auf die pflanzliche Transpiration II. *Ber. schweiz. bot. Ges.* 49 : 555.
 GRADMANN, H. 1928. Untersuchungen über die Wasserverhältnisse des Bodens als Grundlage des Pflanzenwachstums. I. *Jahrb. wiss. Bot.* 69 : 1.
 GREGORY, F. G., F. L. MILTHORPE, H. L. PEARSE & the late H. J. SPENCER. 1950. Experimental studies of the factors controlling transpiration. *Jour. Exp. Bot.* 1 : 15.
 HONERT, T. H. VAN DEN 1948. Water transport in plants as a catenary process. *Disc. Far. Soc.* 3 : 146.
 HUBER, B. 1930. Untersuchungen über die Gesetze der Porenverdunstung. *Ztschr. Bot.* 23 : 839.
 KNIGHT, R. C. 1917. The interrelations of stomatal aperture, leaf water content and transpiration rate. *Ann. Bot.* 31 : 221.
 KNIGHT, R. C. 1922. Further observations on the transpiration of stomata, leaf water content and wilting of plants. *Ann. Bot.* 36 : 361.
 LANDOLT-BÖRNSTEIN 1935. Physikalisch-chemische Tabellen. Dritter Ergänzungsband, erster Teil : 240.
 LARMOR, J. 1918. On transpiration from leaf stomata. *Phil. Mag. and Jour. Sci.*, 6th ser., 35 : 350 and 433.
 LEWIS, F. J. 1948. Water movements in leaves. *Disc. Far. Soc.* 3 : 159.
 LIVINGSTON, B. E. 1906. The relation of desert plants to soil moisture and to evaporation. *Carn. Inst. Wash.* 50.
 LIVINGSTON, B. E. & W. H. BROWN. 1912. Relation of the daily march of transpiration to variations in the water content of foliage leaves. *Bot. Gaz.* 53 : 309.

- LLOYD, F. E. 1908. The physiology of stomata. Carn. Inst. Wash. 82.
- LOTFIELD, J. V. G. 1921. The behaviour of stomata. Carn. Inst. Wash. 314.
- MAXIMOV, N. A. 1931. The physiological significance of the xeromorphic structure of plants. Jour. Ecol. 19 : 273.
- MONSI, M. 1944. Untersuchungen über die pflanzliche Transpiration, mit besonderer Berücksichtigung der stomatären und inneren Regulation. Jap. Jour. Bot. 13 : 367.
- PAETZ, K. W. 1930. Untersuchungen über die Zusammenhänge zwischen stomatärer Öffnungsweite und bekannten Intensitäten bestimmter Spektralbezirke. Planta 10 : 611.
- PENMAN, H. L. & R. K. SCHOFIELD. 1951. Some physical aspects of assimilation and transpiration. Symp. Soc. Exp. Biol. 5 : 115.
- RENNER, O. 1910. Beiträge zur Physik der Transpiration. Flora 100 : 451.
- RENNER, O. 1915. Theoretisches und Experimentelles zur Kohäsionstheorie der Wasserbewegung. Jahrb. wiss. Bot. 56 : 617.
- SEYBOLD, A. 1929a. Die physikalischen Komponenten der pflanzlichen Transpiration. Monogr. aus dem Gesamtgeb. d. wiss. Bot., Berlin.
- SEYBOLD, A. 1929b. Die pflanzliche Transpiration I. Erg. Biol. 5 : 29.
- SEYBOLD, A. 1930. Untersuchungen über die Transpirationswiderstände und über die Temperatur ägyptisch-arabischer Wüstenpflanzen. Planta 9 : 270.
- SEYBOLD, A. 1931a. Weitere Beiträge zur Kenntnis der Transpirationsanalyse I. Planta 13 : 18.
- SEYBOLD, A. 1931b. Weitere Beiträge zur Transpirationsanalyse III. Planta 14 : 386.
- SEYBOLD, A. 1934. Zur Klärung des Begriffes Transpirationswiderstand. Planta 21 : 353.
- SEYBOLD, A. & K. FÜSSER. 1931. Weitere Beiträge zur Transpirationsanalyse II. Planta 14 : 77.
- SHREVE, E. B. 1914. The daily march of transpiration in a desert perennial. Carn. Inst. Wash. 194.
- SHULL, CH. A. 1939. Atmospheric humidity and temperature in relation to the water system of plants and soils. Plant Phys. 14 : 401.
- SIERP, H. & A. SEYBOLD. 1927. Untersuchungen zur Physik der Transpiration. Planta 3 : 115.
- SIERP, H. & A. SEYBOLD. 1929. Weitere Untersuchungen über die Verdunstung aus multiperforierten Folien mit kleinsten Poren. Planta 9 : 246.
- STEFAN, J. 1881. Ueber die Verdampfung aus einem kreisförmig oder elliptisch begrenzten Becken. Sitzungsber. kais. Akad. Wiss. Wien, Mathem.-Naturwiss. Classe, II. Abt. 83 : 943.
- STÄLFELT, M. G. 1927. Die photischen Reaktionen im Spaltöffnungsmechanismus. Flora N. F. 21 : 235.
- STÄLFELT, M. G. 1929. Die Abhängigkeit der Spaltöffnungsreaktionen von der Wasserbilanz. Planta 8 : 287.
- STÄLFELT, M. G. 1932a. Der stomatäre Regulator in der pflanzlichen Transpiration. Planta 17 : 22.
- STÄLFELT, M. G. 1932b. Der Einfluss des Windes auf die kutikuläre und stomatäre Transpiration. Svensk Bot. Tidskr. 26 : 45.
- STÄLFELT, M. G. 1935. Die Transpiration und Kohlensäureassimilation bei Blättern und Stroh des Hafers. Angew. Bot. 17 : 157.
- TRELEASE, S. F. & B. E. LIVINGSTON. 1916. The daily march of transpiring power as indicated by the porometer and by standardized hygrometric paper. Jour. Ecol. 4 : 1.
- VERDUIN, J. 1947. Diffusion through multiperforate septa. Photosynthesis in plants. A Monograph of the Am. Soc. of Plant Physiologists : 95.
- WELTEN, M. 1933. Physiologisch-ökologische Untersuchungen über den Wasserhaushalt der Pflanzen mit besonderer Berücksichtigung der Wasserabgabewiderstände. Planta 20 : 45.
- WIESNER, J. 1887. Grundversuche über den Einfluss der Luftbewegung auf die Transpiration der Pflanzen. Sitzungsber. kais. Akad. Wiss. Wien, Mathem.-Naturwiss. Classe, I. Abt. 96 : 182.
- WRENGER, Maria 1935/36. Über den Einfluss des Windes auf die Transpiration der Pflanzen. Ztschr. Bot. 29 : 257.

MISCELLANEOUS BOTANICAL NOTES V¹

BY

C. G. G. J. VAN STEENIS

Flora Malesiana, Leyden

(Received Febr. 18th, 1953)

39. OCHROCARPUS IN NEW CALEDONIA (Guttif.)

In June 1952 Mr. J. WYATT SMITH, going through Malaysian Calophyllum at Leyden found that some sheets identified as *C. neurophyllum* Schltr. from New Caledonia (Bot. Jahrb. 39, 1906, 193) do not belong to Calophyllum. They were collected by Franc (no. 547) near l'Hermitage, along the border of a stream, Oct. 1906. It appeared they belong to Ochrocarpus.

The sheets were identified by BONATI and certainly fit the type description of SCHLECHTER, though the leaves are somewhat larger viz $10\frac{1}{2}$ –14 × 4–5½ cm and I found 4 petals (Schlechter mentioned 3). Their elliptic-oblong shape suggests that of *O. longifolius* (Wight) B. & H. and not that of *O. odoratus* (Raf.) Merr. (cf. J. Arn. Arb. 26, 1945, 94) which acc. to MERRILL is rather uniform though of wide distribution and formidable synonymy. *O. papuanus* Laut. is different and so is *O. glaucus* Merr. from Samoa, the latter having a glaucous leaf-underside.

Not having the intention to revise the genus, it seems for the present best to keep the species as it is and to transfer it to Ochrocarpus as *Ochrocarpus neurophyllum* (Schltr.) comb. nov.

It is certainly remarkable that no species of the genus, which is widely distributed in the paleotropics from Africa and specially Madagascar through SE. Asia to the West Pacific Islands has yet ever been found in the Australian continent.

40. NOTE ON KJELLBERGIODENDRON CELEBICUM (Koord.)

MERR. (Myrtac.)

After my notes on this genus (Acta Bot. Neerl. 1, 1952, 440–442) had been published some duplicates were received collected by PLEYTE in the N. part of the Island of Misool, West of New Guinea, belonging administratively to the Sorong Division.

¹ The first paper in this series appeared in Bull. Bot. Gard. Btzg III, 17 (1948) 383–411; the 2nd in Blumea 6 (1948) 243–246; the 3rd in Bull. Bot. Gard. Btzg III, 18 (1950) 457–461; the 4th in Reinwardtia 1 (1952) 476–481.

Misool. W of Fakal, bank of Kasim River, scattered, tree 7 m by 6 cm, fl. dirty yellow, fr. reddish, 30 m alt., Oct. 6, 1948, Pleyte 1112; near Waima, common but scattered, in forest, tree 20 m by 15 cm, fl. light yellow, Sept. 26, 1948, Pleyte 1050; ditto, Pleyte 743.

Through a mistake the specimens were accepted to have been collected in Sorong, off the coast of West New Guinea, and the corresponding cross on the map (l.c.) should be transferred a little to the SW to the island of Misool.

41. *CALLITRIS* IN NEW GUINEA (Conif.)

In 1929 the occurrence of *Callitris* (cf. *robusta* R. Br.) was recorded by H. J. LAM in his *Fragmenta Papuana* (Natuurk. Tijd. Ned. Ind. 89, 1929, 304, 354; translated in *Sargentia* 5, 1945, 143, 168) on the basis of a specimen (Lam 2166) on the S. slope of Dika Valley, ca 1250 m alt., dd. 25 Nov. 1920: "treelet on an open deforested slope". This specimen recently came to hand; it is sterile, and apparently of a juvenile plant, but its morphology and anatomy prove it to belong to some species of *Casuarina* sect. *Tetragonae* Poiss.

The geographical area of *Callitris* (Australia, Tasmania, New Caledonia) certainly gives reason to expect it to occur in some parts of New Guinea; I assume this will be rather in the seasonal savannah areas than in the mountains.

42. A NEW EAST MALAYSIAN SPECIES OF *METROSIDEROS* (Myrtac.). Fig. 1-2.

Metrosideros nigroviridis sp. nov. — Arbor glaberrima; ramulis ultimis teretibus aequae ac petiolis in statu sicco nigricantibus; cortice ramulorum haud defoliante. Folia spiraliter ordinata rarissime opposita, in statu sicco laete viridia obovata, in petiolum attenuata, basi aequalia, apice obtusa vel (praecipue in speciminibus sterilibus, foliis majoribus instructis) longiter breviterve obtuse acuminata, 4-5 cm longa, 1½-2½ cm lata (in speciminibus sterilibus usque ad 10 cm longa, 3-4½ cm lata et tunc interdum oblongo-lanceolata); nervi laterales tenues paralleli, sub angulo $\pm 50^\circ$ patententes, ca 12 utrinque (venis tertiariis parallelis interpositis), omnes reticulatim conjuncti, supra haud, infra paululo prominentes; nervus intramarginalis ± 1 cm a margine remotus; petiolus 1-1½ cm longus. Flores cymose ordinati; cymae in inflorescentias axillares terminalesque 1-1½ cm longe pedunculatas unitae, paniculam foliatam folia excedentem, ± 15 cm longam subglobosam efformantes; flores 5-meri; calycis tubus obconicus $\pm 2½$ mm diam., ± 1 mm longus, interdum deorsum stipitiformiter attenuatus; ovarium apice planum; calycis segmenta lata, 1/4-1/3 mm tantum longa; petala basi lata inserta, in alabastro valde imbricata et concava, serius planiora, rotundiuscula, ± 4 mm longa, ± 3 mm lata, sub anthesi patentia. Stamina numerosissima (± 100), libera, duplice tripliceve serie annulatin ordinata, praefloratione inflexa; filamenta manifeste inaequalia (intima breviora)

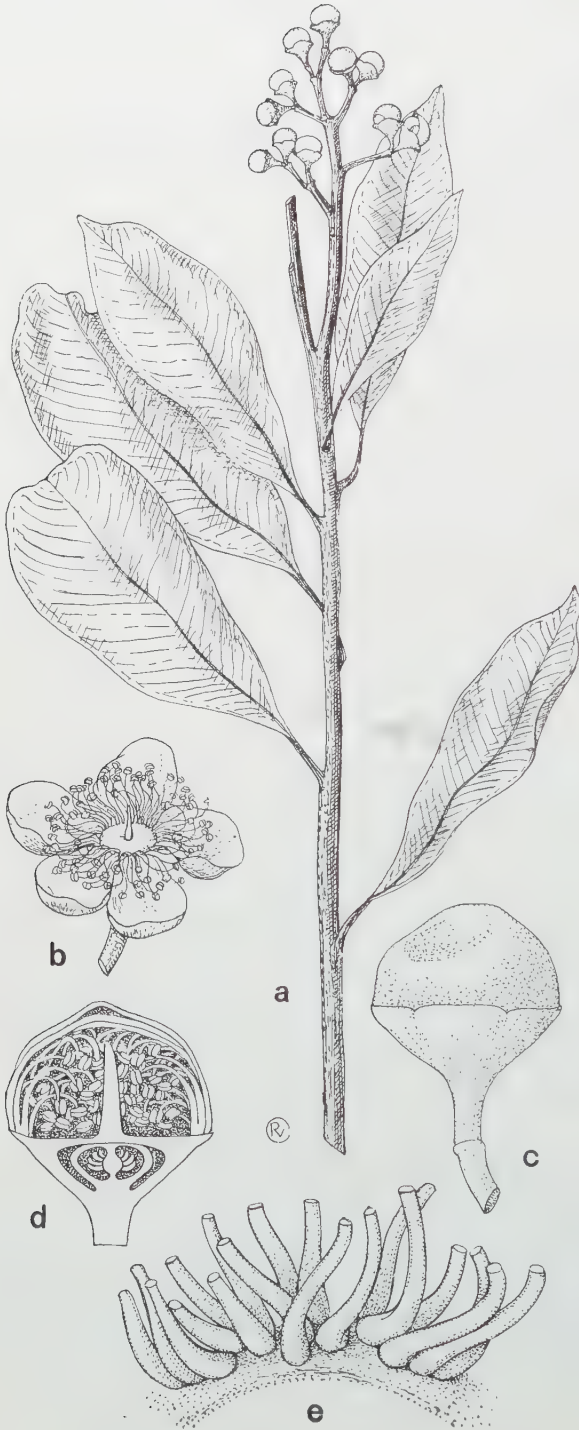


Fig. 1. *Metrosideros nigroviridis* Steen. a. Flowering twig, b. flower in anthesis, c. bud, d. flower in section, e. insertion of stamens (after type specimen, a $\times 5/6$, b—d $\times 5$, e $\times 16$).

2-3 mm longa; antherae dorsifixae, minutae, late ovaes; stylus in alabastro rectus, ± 2 mm longus; stigma punctiforme; ovarium stipite $\frac{1}{2}$ -4 mm longo suffultum, 3-loculare; ovula in singulis loculis numerosa, placentae axili imposita, ascendencia; pericarpium ovarii e stratis pluribus compositiparibus internus ut videtur corneus.

MOLUCCAS. Batjan: Masurung, 500 m, bb. 23144, vern. badenga m \grave{e} rah perempuan; Saoran Domut, 100 m, bb. 23177, vern. palano sela = p. merah; Islet of Kasiruta, near Tawa, bb. 23220, vern. taolat \acute{e} ; ditto, bb. 23224, vern. marinteng utan. Buru: Balo-balo, 250 m, bb. 25168, vern. karihi; Ilat, 150, m bb. 24461, vern. kadien. Ambon: Waai, 100 m, bb. 25976, vern. m \acute{e} rah daun tjenk \acute{e} kulit kasar, K. Ceram: W. Ceram, between Piru and W. Kawa, 400 m, Rutten 1903 (Leyden, typus), fl. 16/11/1918; Loki (W. Ceram), 100 m, bb. 13414, vern. wa \acute{e} asu = m \acute{e} rah daun tjenkeh, K.; E. Ceram, Artafela, 60 m, bb. 25807, vern. tan m \acute{e} rah.

WEST NEW GUINEA. Midden Vogelkop, bb. 22168; Hill N of Hollandia, bb. 25050. Biak Island: Serui, 50 m, bb. 30678, vern. senermus; ditto, Aet & Idjan (Exp. van Dijk) 862, vern. senermus; ditto, bb. 30681, vern. naskain; ditto, bb. 30765, vern. beriek, ai; ditto, bb. 30771, vern. senermus; ditto, bb. 30823, vern. beriek, ai; ditto, bb. 30829, vern. sinar \acute{e} h.



Fig. 2. Localities of *Metrosideros nigroviridis* Steen.

A very typical species with black twigs and lightgreen leaves: the cited specimens, which are sterile except one, show a remarkable conformity. I did not find it described either in *Metrosideros* or in *Tristania*. Duplicate specimens have been distributed under these generic names or as *Kjellbergiodendron* sp. and will be found in several herbaria.

I have tentatively described it in the genus *Metrosideros* in absence of fruit and seed. It is unlike most Malaysian species of *Metrosideros*, but the leaf characters are found in some extra-Malaysian species.

43. SPERMABOLUS T. & B. = ANAXAGOREA ST. HIL. (Annon.)

In 1865 Miquel (Ann. Mus. Bot. Lugd. Bat. 2, p. 22, t. 2) published the description and a figure of a plant from Batjan Island, Moluccas, which he had received from the curators of the Botanic Gardens,

Buitenzorg, J. E. Teysmann & S. Binnendijk, under the name of *Rhopalocarpus fruticosus* T. & B. as belonging to the Annonaceae.

Both he and the authors were unaware that the generic name *Rhopalocarpus* was already occupied by a genus *Rhopalocarpus* Bojer described from Madagascar. The latter name was originally published as a nomen nudum (Bojer, Hort. Maurit. 1837, p. 44) and in wrong orthography (*Rapolocarpus*). Subsequent authors corrected this name to *Ropalocarpus*, until Bojer gave his final diagnosis (Trav. Soc. Hist. Nat. Ile Maurice 1846, p. 149; cf. Hook. Icon. Plant. 1900, t. 2774), in which the origin of the intended name *Rhopalocarpus* was explained. This publication must be regarded as the valid publication of Bojer's. The genus was originally referred to Tiliaceae, later also to Flacourtiaceae, and is now mostly regarded as belonging to a separate family Rhopalocarpaceae.

Rhopalocarpus T. & B. ex Miq. was rightly reduced to the genus *Anaxagorea* by Bentham & Hooker (Gen. Pl. 3: 957).

One of the authors, S. BINNENDIJK, had in the meantime discovered the pre-occupation of the name *Rhopalocarpus* and had changed it into *Spermabolus*. He had, in the Botanic Gardens, Buitenzorg, given the type-plant a new name, *Spermabolus fruticosus* (T. & B. ex Miq.) T. & B. This he wrote in an unpublished letter dated July 25th, 1864 (preserved at the Leyden Bot. Garden), to the curator of the Leyden Botanic Gardens, H. Witte, whom he had sent a living plant for the greenhouse.

The name *Spermabolus* was published by TEYSMANN & BINNENDIJK as a new generic name (nomen nudum) in the third Catalogue of the Bot. Gardens, 1866, p. 178 and referred to the Magnoliaceae! No synonym was cited. As such it was inserted in the Ind. Kew. and in De Dalla Torre & Harms, Gen. Siph.

However, SCHEFFER had already published its true status under *Anaxagorea fruticosa* (T. & B. ex Miq.) Scheff. in Natuurk. Tijd. Ned. Ind. 31, 1869, p. 9; transl. in Flora 52, 1869, p. 302. And BOERLAGE had thirty years later reduced the names of TEYSMANN & BINNENDIJK and of SCHEFFER to *Anaxagorea luzoniensis* A. Gray (Ic. Bog. 1, 1899, p. 108).

44. A NEW AMORPHOPHALLUS FROM JAVA (Arac.). Fig. 3.

Amorphophallus sagittarius n. sp. — Folia in specimine unico viso haud bulbillifera, petiolo \pm 34 cm longo sustenta; segmentis primariis lateralibus petiolulis 5–7 cm longis suffultis, semel furcatis; foliola totaliter 14, oblique oblonga, basi haud alatiforme decurrentia, manifeste caudato-acuminata, nervo marginali subundulato, 6–17 cm longa, $2\frac{1}{2}$ –6 cm lata. Tuber subglobosum subdepressum, 4–5 cm latum, 3–4 cm altum. Pedunculus \pm 12 cm longus, \pm 8 mm crassus, basi munitus squamis plurimis vaginiformibus appressis brunneis, quarum intima ceteris longior pedunculum subaequans. Spatha spadici subaequilonga, ovata, obtusa, expansa ca 13 cm longa, \pm 10 cm lata, extus basin versus pallida, juxta marginem superiorem intense

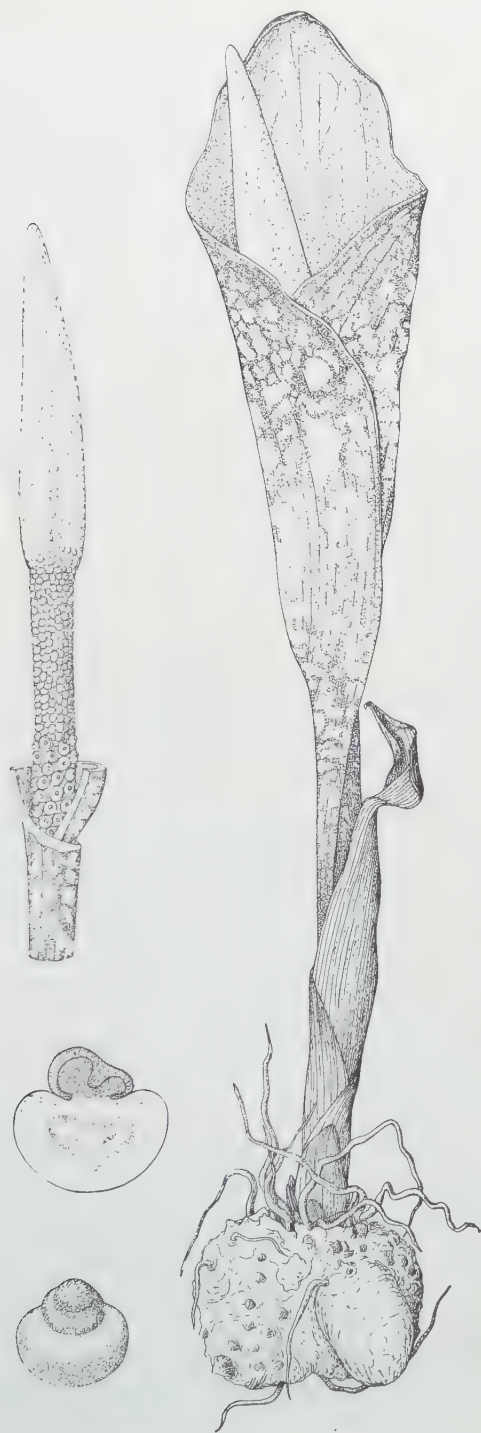


Fig. 3. *Amorphophallus sagittarius* Steen. Plant and spadix, $\times \frac{1}{2}$, ovary $\times 3$, ditto, in section, $\times 5$.

purpureo-olivacea, maculis pallide viridibus conspersa. Spadicis pars ♀ cylindrica ca 1½ cm longa, ± 8 mm crassa; ovaria intervallis sejuncta, subdepresso-globosa, viridia, 1-ovulata, 3 3¼ mm lata; stigma sessile, capitatum integrum, ± 1½ mm diam.; spadicis pars ♂ subcylindrica, superne paullulo incrassata, ± 3½ cm longa, 8 mm lata; antheris confertis pallide aurantiaca, ± 2 mm longa, ± 1 mm lata. Appendix sterilis lanceolata, cremicolor, minute tuberculata, ± 7 cm longa, medio bene 1 cm lata.

Typus: L. van der Pijl 899a, ins. Java occid. pr. Tjisadea, 8/11-1941 (Bo).

Among the many living specimens of *Amorphophallus* received before the war at Bogor for identification, I failed to classify the specimen cited above with any species hitherto described. In determining it with Backer's excellent key of the Javan species (Trop. Natuur 9, 1920, 21-32) it is by its uniovulate ovaries nearest to *A. spectabilis* (Miq.) Engl., which I have personally collected on several occasions. This is distinctly different by its size, by the size, shape and colour of the spathe, and by the shape and relative dimensions of the spadical parts (♀, ♂, and appendix).

It is apparently closer related to two Sumatran species, viz *A. cobra* v.A.v.R. and *A. obovoideus* v.A.v.R.

Both differ, however, by the spathe exceeding the spadix, and the different shape of the appendix. In passing, it may be remarked that the latter two species appear to me to be conspecific.

It might be assumed that the new species is conspecific with the obsolete *A. giganteus* Bl. which is depicted as having an inflorescence of a similar habit, and which has never been found again in Java since BLUME described it (Rumphia 1, p. 144, t. 34). Apart from the fact that Backer assumes that Blume's description is based on leaves from one and an inflorescence from another species, BLUME's figure shows distinctly bilocular ovaries whereas the new species possesses only one ovule and one cell.

Prof. Dr L. van der Pijl unfortunately lost the pre-war specimens which he cultivated at Bandung; he wrote me that the specimens at Bandung developed glossy, brown purple spathes, a change in colour which he observed also in some *Arisaema* species in cultivation.

Measurements in the description above have been taken from the living plant.

45. SOME NEW RECORDS OF NEW GUINEAN PLANTS

Dumasia villosa DC. (Papil.). Widely distributed from Africa through SE. Asia to Malaysia; hitherto the Eastern border of this genus was Luzon-Celebes-Lombok.

East New Guinea, Mt. Hagen Distr., Wahgi Valley, Nondugl, ca 1600 m, Aug.-Nov. 1951, Countess Greta Gyldenstolpe s.n. (S).

Drosera peltata Sw. (Droserac.). Widely distributed from Australia through Malaysia to SE. and E. Asia, in the montane area,

in Malaysia primarily in regions subject to a distinct dry season. One of the New Guinea localities is very high and certainly not situated in a seasonal climate.

New Guinea. Western part: grasslands, common on wet peaty soil containing a good deal of sand, plant red, flowers white, Lake Habbema, 3225 m, Aug. 1938, Brass 9195 (A, L). Eastern part: Plateau north base of Mt Giluwe, Central Highlands, near waterways, May 15, 1951, 2200 m, F. Shaw Mayer (BM).

Protium macgregorii (F. M. Bailey) comb. nov.¹ (Burser.). — *Bursera macgregorii* F. M. Bailey, Queensl. Agric. J. 3 (1898) 282. — *Santiria schlechteri* Laut. Bot. Jahrb. 56 (1920) 333. — *Protium schlechteri* Leenh. Blumea 7 (1952) 157.

Type specimen: SE. Papua, pr. Taupota, V-1898, Sir William MacGregor s.n. (Bri).

Miss L. M. PERRY kindly pointed my attention to Bailey's description which had not been recognized earlier in burseraceous studies. Mr FRANCIS kindly sent on loan the type specimen which appeared to be conspecific with LAUTERBACH's species. MACGREGOR's specimen bears female flowers and one fruit. The flowers are 5-merous, not 6-merous as BAILEY erroneously mentioned. The species seems to be confined to New Guinea and represents the only species of the genus in the island.

46. SOME NOTES ON EASTERN BIGNONIACEAE

Bignonia comosa Roxb., Hort. Beng. (1814) 95, nom.nud.; Fl. Ind. ed. Carey 3 (1832) 103; DC., Prodr. 9 (1845) 144; Miq., Fl. Ind. Bat. 2 (1858) 751. — *Spathodea ?comosa* G. Don, Gen. Syst. 4 (1838) 222.

The identity of this species, described from the Moluccas, has up till now remained obscure. An authentic specimen (possibly an isotype) is present at Brussels, in the herbarium of v. Martius, with Roxburgh's handwriting and addition of the number "2652". However, this sheet, which was kindly loaned by Prof. ROBIJNS, does not wholly confirm to the description; it consists of a leafy twig, and a detached fruit, whereas the description points to leaves and flowers only. On the other hand the leaves *exactly* match the description. Both Dr MERRILL and I myself are of the opinion that the leaves doubtless represent a *Clerodendrum* (Verbenaceae). The capsule apparently belonging to a separate small label on which is written: "Capsule of No 14 Pou Madyro an Bignonia", we find doubtless bignoniaceous (but not *Bignonia chelonoides*, Roxb. l.c. 106), and I can add that it belongs to a species which is certainly not native in Malaysia, but presumably in SE. Asia. I assume the pod was added later, anyhow erroneously to the sheet, as it was not mentioned in the type description. The leaves, therefore, should be taken as typifying Roxburgh's species.

In verifying these leaves with the Rijksherbarium collections I have

¹ This note is by Mr P. Leenhouts, Rijksherbarium, Leyden.

found them *exactly* matching those of *Clerodendrum lanuginosum* Bl. (1825). *Bignonia comosa* Roxb. is therefore to be added to the synonymy of the latter.

Nyctocalos brunfelsiiflorus T. & B. ex Miq. in Journ. Bot. néerl. 1 (1861) 367.

Borneo. North Borneo: near Kudat, Jan. 1885, M. Fraser 113 (K), in fruit; near Niah, June 1894, on limestone, Haviland & Hose 3539 (K), in flower.

This is an interesting new locality of a very rare local-endemic Javanese species and one of the very few instances of plants known only from Borneo and Java.

Nyctocalos pinnata Steen. n. sp. Folia 5-foliolata; foliolo secundario parvo nonnunquam adjecto uni ex foliis paris infimi; petiolus 4–5½ cm longus; rachis 4 cm; foliolis petiolulis 2–11 mm longis (petiolulo folioli terminalis \pm 2½ cm longo) suffultis, e basi inaequaliterali ovatis vel ovato-oblongis obtuse acuminatis 6–8 cm longis 2–4 cm latis, penninerviis, nervis lateralibus utrinque 4–6. Flores incogniti, probabiliter iis *N. cuspidatae* et *N. shamicae* similes; calyx fructifer 5 mm altus, glandulosus, 5-dentatus; dentibus singulis infra apicem corniculo munitis. Capsula basi in (pseudo) stipitem 2 cm longum angustata, oblonga, acute acuminata, plana, 13–15 cm longa (stipite haud computato) 4½–5 cm lata; valvulis carinatis. Semina (ala haud computata) reniformis emarginata 1¼ cm longa, 1 cm lata, circumdato ala annulari 2 cm lata; ala terminata margine tenui hyalino, \pm 1½ cm lato; pars seminifera excentrica; semen totum \pm 3½ cm diam.

China. Yunnan: Hzen-hu, Ma-an-shen, large climber, 1500 m alt., Henry 13408 (typus, K; NY).

The affinity of this species, the third to be reported from the Asiatic continent and the first from China, is not clear as flowers are not present. The fruit differs much from the linear capsule of *N. brunfelsiiflorus*. The leaves are much smaller than those of *N. thomsoni*, and it seems that the alliance is definitely with *N. cuspidatum*. From all species hitherto known it differs in the 5-foliolate leaves. The horn-like appendages on the back of the calyx-teeth are conspicuous.

Radermachera bipinnata (Coll. & Hemsl.) Steen. ex Chatterjee in Bull. Bot. Soc. Beng. 2 (1948) 71. — *Tecoma ?bipinnata* Coll. & Hemsl. J. Linn. Soc. 28 (1890) 102. — *Radermachera alata* P. Dop, Bull. Mus. Paris 32 (1926) 184; Fl. Gén. Indo-Chine 4 (1930) 584, fig. 36 1–2, syn. nov.

Upper Burma. Shan Hills, Lwe-kaw, 1200 m, May 1888, Collett 685 (typus, K), leaves immature, no fruits; Ruby Mine District, J. W. Oliver 166 (K); Wa States Panyan Ywa, April 30, 1937, Po Khant 15334 (K).

Yunnan. Szemao, Eastern Mts, 1800 m, Henry 13020 (K); same place, Western Mts, 1500 m, Henry 12447 (K).

Up till recently this species had been referred to the collective genus *Tecoma*. The additional collections allow to complete the original description: Shrub or treelet, 8–18 feet. Leaves up to 35 cm long; rhachis distinctly winged; leaflets puberulous underneath and glandular towards the base. Inflorescences hanging, in slender long-peduncled (1)-2-(3)-flowered cymes, 10–15 cm long, not branched, more or less ramiflorous to distinctly cauliflorous. Pedicels thin. Bracts narrow-lanceolate, 5 mm long. Corolla rather long-tubular, straight, yellow (ex Henry). Disk cupular. Ovules pluiseriate. Capsules terete, falcate, 20–25 cm long, 6–7 mm diam.; septum thin, perpendicular to the valves, with two rows of scars on either side. Seeds thickish, woody-corky, outside convex, more or less imbricate with the sharply wedge-shaped margins, in each cell distinctly in two rows.

Now that its fruit characters are known, it appears that this species occupies a singular position within the genus *Radermachera*. Its hanging, ramiflorous, unbranched inflorescences and narrowly winged leaf-rhachis it shares with *R. ramiflora* Steen. from Borneo (J. Bot. 72, 1934, 5), but in its fruit characters: a thin septum, unwinged, thick seeds of which only two rows develop in each cell, it deviates from all other species hitherto described. Therefore, it seems necessary to regard it as typifying a special section within the genus which I divide as follows.

Sectio Alatae, sect. nov. — Semina alata.

Typus: *R. gigantea* (Bl.) Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 250.

Sectio Exalatae, sect. nov. — Semina exalata.

Typus: *R. bipinnata* (Coll. & Hemsl.) Steen. ex Chatterjee.

The genus *Radermachera* has been enriched during the last two decades with a relative large number of species described from various countries in Southeast Asia and Southern China, among which are several morphologically very interesting species. The centre of speciation and morphological diversity lays definitely in Southeastern Asia, as the Malaysian species are mutually closely related. The species treated above accentuates this picture. A close ally of *Radermachera* seems to be the equally SE. Asiatic, monotypic genus *Mayodendron* which differs from *Radermachera* by 2 rows of ovules in each cell (against many), a distinct longitudinal "false dissipation", and a spathaceous calyx. Its habit is, however, very similar to that of a *Radermachera* and a closer study may show that it represents a distinct section of *Radermachera*.

Radermachera glandulosa (Bl.) Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 250. — *Spathodea glandulosa* Bl., Bijdr. (1825) 763.

China. Kwangsi: W. T. Tsang 22326.

This is apparently a new record for China.

PORPHYRA LEUCOSTICTA ALONG THE DUTCH COAST

BY

C. DEN HARTOG

Hugo de Vries Laboratory, Amsterdam

(Received March 6th 1953)

Since VAN GOOR's publication "Die Holländische Meeresalgen" appeared in 1923, the marine algae flora of Holland has not received much critical study. Since the war, however, the interest in this subject increased, and we have started a survey of our coast. During this work algae which had not been known to occur in our waters were found regularly. Probably this was because they were collected in localities which had never been investigated before. It may be assumed that some of the newly found species had settled here only a short time ago, while other species had probably been overlooked.

Porphyra leucosticta e.g. is a species which has been washed ashore on our beaches since the days of old (i.a. 1844), but had never been recognised before. In the province of Zeeland this species now has been discovered as an autochthonic. There it forms a very characteristic association together with *Monostroma wittrockii* Bornet.

Porphyra leucosticta Thuret in Le Jolis, Alg. mar. de Cherbourg, 1863, p. 100; Børgesen, Bot. Faerøes, 1903, p. 346; Kolderup Rosenvinge, Mar. alg. Denm. I, 1909, p. 65, Pl. II fig. 4-13; Woronichin, Trav. Soc. Imp. Nat. de St. Pétersbourg vol XL, 1909, p. 180; Hamel, Rev. Alg. I, 1924, p. 438, fig. V; Newton, Handb. Brit. Seaweeds, 1931, p. 240; Feldmann, Rev. Alg. XI, 1939, p. 248. *Porphyra atropurpurea* De Toni (non Olivi), Syll. Alg. IV sect I, 1891, p. 17; VI sect 5, 1924, p. 9; Lakowitz, Algenfl. ges. Ostsee, 1929, p. 300, fig. 409; Hoffmann, Wiss. Meeresunt, Kiel, XXI, 1931, p. 9. *Porphyra elongata* (Aresch). Kylin, Stud. Algenfl. schwed. Westk., 1907, p. 110, Pl. 3, fig. 1; De Toni, Syll. Alg. VI, sect 5, 1924, p. 8.

In *Porphyra leucosticta* the spermatia are formed in small longitudinal patches, specially in the upper part of the thallus, often parallel with the margin. The length of these patches is rather variable. ROSENVINGE (1909) and NEWTON (1931) give 5-10 mm, but in the Dutch specimens I have found sizes ranging from 1.5 to 20 mm. The breadth varies from 1-2 mm which agrees with the data given in literature. The spermatangia of the Dutch specimens have very irregular forms. This

is in accordance with the statement of BØRGESSEN (1903) from the Faerøes, who found broader and more irregular antheridial sori in this species than he observed in specimens from France. He also stated that the arrangement of the sori was more irregular. Probably he compared his specimens with samples from the Mediterranean coast, for HAMEL (1924) distinguished two forms in the French material of *Porphyra leucosticta*, viz. an Atlantic and a Mediterranean form. The differences are:

- f. *atlantica*: Large Alga, up to 35 cm long. Irregularly formed, rather large spermatangia grouped along the margin of the frond.
- f. *mediterranea*: Smaller Alga, up to 20 cm. The spermatangia often stretch towards the centre of the thallus; they are narrow and linear, so that the thallus sometimes looks striped.

The specimens found on the Dutch coast are to be classified as



Fig. 1. *Porphyra leucosticta* Thuret f. *atlantica* Hamel from the Zuid Beveland Canal

f. *atlantica*. The samples from the Faeröes may belong to this form, too. The type specimen of THURET (1863) belongs to the Atlantic form as well; in the diagnosis THURET described the spermatangia as "antheridiis in soris maculiformibus dispositis". The carpogonia are found scattered between the antheridia, so the alga is monoecious.

The frond, which is very short stalked, is attached with a disc and often umbilicate. The margin of the thallus is undulate.

In the Dutch waters *Porphyra leucosticta* does not reach the dimensions given by HAMEL (35 cm) and NEWTON (10–40 cm). The largest specimen, collected in an autochthonic locality, measured 12 cm in length. On drifting objects specimens 14–15 cm long are found. Also in Denmark ROSENVINGE (1909) only found specimens of 10–11 cm (–16).

The colour of the thallus is of a much brighter purple than that of *Porphyra umbilicalis* (L.) J. Ag. ROSENVINGE pointed out, however, that both species may occur with exactly the same colour. Another character, apparently not mentioned in the literature, is that *Porphyra leucosticta* adheres very easily to paper, while *Porphyra umbilicalis* does not, although this difference is not absolute.

FELDMANN (1939) pointed out, that *Ulva atropurpurea* Olivi 1793 is not a synonym of *Porphyra leucosticta* Thur., as was assumed by De Toni (1891), but it is probably identical with *Porphyra umbilicalis* (L.) J. Ag. In this article therefore the name given by THURET is used since it is the oldest legitimate one.

Porphyra elongata (Aresch.) Kylin cannot be separated specifically from *Porphyra leucosticta*. According to KYLIN (1907) the two species are related because both are monoecious and in both the antheridia occur in distinct sori. *Porphyra elongata*, however, should have an elongated, equally broad frond, a thickness of thallus of 25–33 μ and smaller (to 2 mm) antheridial sori. These differences, however, cannot be maintained.

Porphyra leucosticta is often elongated. The thickness of the thallus was found 28–44 μ which is in accordance with the statement of ROSENVINGE (1909). KYLIN, however, gives 33–40 μ . Since specimens of *Porphyra leucosticta* with very small antheridial sori were seen together with larger ones, ranging from 1.5 to 4 mm, *Porphyra elongata* is, in the writer's opinion merely a young form of *Porphyra leucosticta*, in which the antheridial sori are beginning to differentiate.

Summarizing the differences between *Porphyra leucosticta* and *Porphyra umbilicalis*, a common species along the whole Dutch coast, we get:

<i>Porphyra leucosticta</i> Thuret	<i>Porphyra umbilicalis</i> (L.) J. Ag.
Spermatia formed in longitudinal patches.	Spermatia formed in the marginal zone of the frond.
Monoecious.	Dioecious, sometimes monoecious, but then the antheridia and carpogonia are strictly separated.

GEOGRAPHICAL DISTRIBUTION

Porphyra leucosticta Thuret is very widely distributed in the Mediterranean (French coast, Algiers, Corsica, Tangier, Naples, Adriatic Sea, according to FELDMANN, 1939) and is met with in the Black Sea, too (WORONICHIN, 1909).

In the Atlantic the species is known from the Canary Islands to the West coast of Sweden and the Faeröes. It is even found in the Baltic Sea (HOFFMANN, 1931). BØRGESSEN and JONSSON (1908) as well as FELDMANN (1939) state the occurrence of *Porphyra leucosticta* on the Atlantic coast of North America. There are in the collection of the Rijksherbarium, Leiden, some American specimens, but in the writer's opinion they are not identical with the European form. In the same herbarium there are some specimens, collected in Japan.

PHAENOLOGY

In almost the whole of its area *Porphyra leucosticta* behaves as a winter species. It begins to develop in autumn, in the early spring it reaches its highest development, and towards the end of spring it disappears. In literature the following phaeonological data were found.

Mediterranean	October–May–June	FELDMANN, 1939
French West coast	December–April–June	HAMEL, 1924
Great Britain	spring and early summer	NEWTON, 1931
Netherlands	October–April	
Denmark	April–July, disappearing in summer	ROSENVINGE, 1909
Baltic Sea	October–July	HOFFMANN, 1931
Swedish West coast	July–August	KYLIN, 1907
Faeröes	April–August	BØRGESSEN, 1903

So we can say that the growth period is longer the farther north the locality is situated. It is very likely that in Great Britain and Denmark the species also occurs in autumn, but no statement on this subject was found.

BØRGESSEN and KYLIN only mentioned the seasons in which they found fructifying specimens, not the entire growth period. In the Dutch specimens I found organs for sexual reproduction in autumn as well as in spring.

DISTRIBUTION OF PORPHYRA LEUCOSTICTA ALONG THE DUTCH COAST

Up to the present *Porphyra leucosticta* has never been recognized on the Dutch coast. In 1950 and 1951 the species was discovered as an autochthonic as well as on drifting objects. We distinguish sharply between the two categories. The algae, growing on our coasts, belong to the Dutch flora, but the algae washed ashore, the *natural adventives*, may be transported by the wind and sea currents over a distance of hundreds of miles before they reach the coast. Among these algae there are many species which are never found growing attached on the Dutch coast, e.g. *Himanthalia elongata* (L.) Setchell, *Halidrys siliquosa* (L.) Lyngb., *Cystoseira* species, *Rhodymenia palmata* (L.) Grev. and many others.

a. *Finds on drifting objects:*

After the gale of Easter 1950 a great quantity of drifting algae, chiefly consisting of *Himanthalia elongata*, *Fucus vesiculosus* L., *Ascophyllum nodosum* (L.) Le Jol. and *Halidrys siliquosa* were washed ashore along the whole beach of the province of North Holland. The southern origin of this material could be ascertained as among the algae there were four species which are not known growing north of the Channel, viz. *Cystoseira fibrosa* (Huds.) Ag., *Cystoseira granulata* Ag., *Gastroclonium ovale* (Huds.) Kütz. and *Antithamnionella sarniensis* Lyle (VAN GOOR, 1923; LUCAS, 1950). Among the numerous epiphytes on the Fucaceae *Porphyra leucosticta* was found a few times. The exact data are:

Den Helder, 12-IV-'50, on *Fucus vesiculosus* and *Polysiphonia lanosa* (L.) Tandy, Den Hartog;

Huisduinen, 14-IV-'50, on *Fucus* and *Polysiphonia lanosa*, Lucas and Swennen.

Beach between Callantsoog and Petten, 14-IV-'50, on *Fucus vesiculosus* and *Himanthalia elongata*. The largest specimens, which were collected, measured 14-15 cm, Den Hartog.

In the spring 1951 only a few algae and other drifting objects were washed ashore; nevertheless *Porphyra leucosticta* was found, together with a number of other algae. This material had a southern origine too, for *Cystoseira fibrosa* and *Halopitys incurvus* (Huds.) Batt., both species with a southern distribution, were present. The substrates on which *Porphyra leucosticta* was collected are given underneath.

Katwijk, 26-III-'51, on *Himanthalia elongata*, Lucas.

Den Helder, 29-III-'51, on an inner shell of *Sepia officinalis* L. and on *Fucus vesiculosus*, Den Hartog.

Beach between Huisduinen and Groote Keeten, 3-IV-'51, on *Ascophyllum nodosum*, *Fucus vesiculosus*, and an inner shell of *Sepia officinalis*, Den Hartog.

Beach between Castricum and Wijk aan Zee, 5-IV-'51, on *Ascophyllum nodosum* and *Polysiphonia lanosa*, Stock.

IJmuiden, 19-IV-'51, on a bunch of cork, Scharrer.

In the collection of the Rijksherbarium there seems to have been some material of older date under the name of *Porphyra vulgaris* Ag.:

Zandvoort, I-1844, on *Chorda filum* (L.) Stackh., Buse.

Scheveningen, without date, on a ship's mast, Vrijdag Zijnen.

In his list of algae from drifting objects LUCAS (1950) published these finds as *Porphyra lacineata* (L.) J. Ag. The two other records of *Porphyra lacineata*, of more recent date given by him also are to be classified as *Porphyra leucosticta*:

Beach between Noordwijk and Noordwijkerhout, 20-I-'49, on a bunch of cork, Lucas.

Beach between Noordwijk and Katwijk, 15-IX-'49, on a branch, Lucas.

b. *Find in an autochthonic locality:*

Spring 1951: (22-III) *Porphyra leucosticta* was found in great numbers by MULDER and SWENNEN in the Zuid Beveland Canal. Autumn 1951: (25-X) MULDER and the author visited this locality; now there were only a few specimens of *Porphyra* present. Spring 1952: (13-IV) MULDER and DE VUYST visited the canal again; the species now proved to be rather common.

This locality had already been surveyed by MULDER and the author in August 1950, but at that time we had not seen any *Porphyra*; nor had the species been observed by MULDER in August and September 1951 nor by the author in July 1952.

ECOLOGY

The Zuid Beveland Canal is a sea-water canal, shut off from the sea by locks, so that no tidal movements occur in it. Still we can distinguish three algal zones.

At the top *Ulothrix subflaccida* Wille (= *U. implexa* Kütz.) forms a 10-20 cm wide belt, in which it is accompanied by *Rhizoclonium riparium* (Roth) Harv. This vegetation is moistened only by rain and when a heavily loaded ship passes.

The second belt is ca. 50 cm wide and coincides with the wavedashed zone. It is characterized by the dominance of *Enteromorpha compressa* (L.) Grev. *Porphyra leucosticta* and *Monostroma wittrockii* Bornet are limited strictly to this belt.

Under it lies a zone which is unaffected by the waves, and is continually submerged. Among the great number of algae, occurring in this belt are: *Chondrus crispus* (L.) Stackh., *Polysiphonia demudata* (Dillw.) Kütz., *Polysiphonia nigrescens* (Dillw.) Grev., *Dasya pedicellata* (Ag.) Ag., *Gracilaria confervoides* (L.) Grev., *Griffithsia devoniensis* Harv., *Callithamnion* species, *Giffordia sandriana* (Zanard.) Hamel, *Bryopsis plumosa* (Huds.) Ag., etc.

The composition of this algal vegetation bears a distinctly southern stamp.

Although BRAUN-BLANQUET (1928) has elaborated his system only for land and fresh water vegetations the writer has tried, just as KORNAŚ and MEDWECKA-KORNAŚ (1950) did, to apply his methods to vegetations of marine algae. This investigation has not yet been finished, but still it seems to be a fact that the *Enteromorpha*-belt of the sea-water canals of the province of Zeeland presents a separate vegetation type. In Holland *Monostroma wittrockii* is limited almost entirely to these canals. So we can consider *Porphyra leucosticta* and *Monostroma wittrockii* as characteristic species of an association for which the writer proposes the name *Monostrometo-Porphyretum leucostictae*. This association is confined to the wavedashed zone of a coast, which is not subject to tidal movements. A survey of this association is given below.

MONOSTROMETO-PORPHYRETUM LEUCOSTICTAE ass. prov.

Zuid Beveland Canal, eastern bank, ca. 50 m south of the Schore-bridge. 25-X-51; Area: $(30 \times 0,5) = 15 \text{ m}^2$, Exposition: west; Inclination 15° ; Depth: 0–20 cm, Coverture: 65 %.

Characteristic species:

<i>Monostroma wittrockii</i> Bornet	1.2
<i>Porphyra leucosticta</i> Thuret f. <i>atlantica</i> Hamel	+

Other species:

<i>Enteromorpha compressa</i> (L.) Grev.	4.4
<i>Enteromorpha tubulosa</i> Kütz. ¹⁾	+2
<i>Ulva lactuca</i> L.	+
<i>Ulothrix subflaccida</i> Wille	+
filiform diatoms	3

Appreciation is expressed to A. VAN DER WERFF, who investigated a sample of diatoms from this survey. He found chiefly the following species: *Navicula crucigera* (W.Sm.) Cl., *Amphipleura rutilans* (Trent.) Cl. and *Navicula gracilis* Ehr., which form filamentous colonies. Among them were found many *Synedra tabulata* (Ag.) Kütz., *Melosira nummuloides* (Dillw.) Ag., *Achnanthes longipes* Ag., and a number of other species. On *Porphyra leucosticta* many little clusters of *Synedra tabulata* were attached.

REFERENCES

- BØRGENSEN, F. The Marine Algae of the Faeröes. Botany of the Faeröes, Vol. II, p. 339–532, 1903.
- BØRGENSEN, F. The Algae-Vegetation of the Färöese Coasts with remarks on the Phyto-Geography. — Botany of the Faeröes, Vol. III, p. 683–834, 1905.
- BØRGENSEN, F. and H. JONSSON. The Distribution of the Marine Algae of the Arctic Sea and of the Northernmost Part of the Atlantic. — Botany of the Faeröes, Vol. III, p. 1–XXVIII, 1908.
- BRUN-BLANQUET, J., Pflanzensoziologie. Berlin, 1928.
- DANGEARD, P., Sur le développement des spores chez quelques Porphyra. — Trav. crypt. vol. jubil. L. Mangin, p. 85–96. Paris, 1931.
- DREW, K. W., Conchocelis-Phase in the Life-History of *Porphyra umbilicalis* (L.) Kütz. — Nature, vol. 164, no. 4174, p. 748–749, 1949.
- FELDMANN, J., Les Algues Marines de la Côte des Albères. — Rev. Alg. vol. X, p. 1–340, 1938; vol. XI, p. 247–330, 1939.
- GOOR, A. C. J. VAN, Die Holländische Meeresalgen. — Verh. Kon. Akad. Wetensch. Amsterdam, 2e sect., vol. XXIII, 2, 1923.
- HAMEL, G., Floridées de France II. — Rev. Alg. I, p. 427–457, 1924.
- HOFFMANN, C., Über eine in der Kieler Förde neu aufgetretene Rotalge: *Porphyra atropurpurea* (Oliv.) De Toni. — Wiss. Meeresunt. Abt. Kiel, vol. XXI, p. 1–9, 1931.
- JOLIS, A. LE, Liste des Algues marines de Cherbourg. — Paris, 1863.
- KORNAŚ, J. and A. MEDWECKA-KORNAŚ, Associations végétales sous-marines dans le Golfe de Gdańsk. — Vegetatio, Vol. II, no. 2–3, p. 120–127, 1950.
- KOSTER, J. TH., Rare and otherwise interesting marine Algae from the Netherlands. — Acta Bot. Neerl. Vol. I, no. 2, p. 201–215, 1952.
- KYLIN, H., Studien über die Algenflora der schwedischen Westküste. — Thesis Uppsala, 1907.
- LAKOWITZ, K., Die Algenflora der gesamten Ostsee. — Gdańsk, 1929.

¹ I am much indebted to Dr J. TH. KOSTER, who identified this Alga.

- LUCAS, J. A. W., The Algae transported on drifting objects and washed ashore on the Netherlands' Coast. — *Blumea*, vol. VI, no. 2, p. 527-543, 1950.
- NEWTON, L., A Handbook of the British Seaweeds. — London, 1931.
- ROSENVINGE, L. KOLDERUP, The Marine Algae of Denmark I, - K. Danske Vidensk. Selsk. Skr. 7, Raekke VII, no. 1, 1909.
- TONI, G. B. DE, Sylloge Algarum omnium hucusque cognitarum. — Padua, 1889-1924.
- WORONICHIN, N. N., Die Rhodophyceen des Schwarzen Meeres. (in Russian) Trav. Soc. Imp. Nat. de St. Pétersbourg, vol. XL, p. 173-356, 1909.

CERAMIMUM DIAPHANUM (LIGHTF.) ROTH,
ITS VARIETIES AND FORMS AS FOUND
IN THE NETHERLANDS

BY

J. A. W. LUCAS
Rijksherbarium, Leiden

(Received March 6th, 1953)

INTRODUCTION

The genus *Ceramium* is one of the most difficult genera of the Algae. The species vary a great deal and, even when the differential characters are carefully chosen, still are connected by transitions. Moreover, there is a strong reticulate relationship within the genus, and henceforth there exists a great diversity of opinion regarding the limits of taxa of various ranks. The author is much indebted to the directors of the "Rijksherbarium" at Leiden, the Botanical Museum at Copenhagen, the "Universitets Botaniska Museum" at Lund, "Botaniska Museet" at Uppsala, as well as to Dr L. G. SJÖSTEDT, who have rendered it possible to study a number of types, viz. of Kützinger, Kylin, Petersen and Sjöstedt. Unfortunately, there was no possibility of studying the types of *Ceramium diaphanum* (Lightf.) Roth var. *diaphanum*, var. *tenuissimum* Roth* and f. *corticatulo-strictum* Kylin. It is to be regretted that Petersen failed to indicate type-specimens. The result is that the type-collections of his taxa are sometimes very extensive.

The author is also much indebted to the directors of the "Rijksherbarium" at Leiden (L.), the "Zoölogisch Station" of the "Nederlandsche Dierkundige Vereeniging" at Den Helder (N.D.V.) and the herbaria of the Universities of Amsterdam (A.) and Utrecht (U.) for putting at his disposal their Netherlands' material of *Ceramium diaphanum* (Lightf.) Roth. It is a great pleasure to the author to express his particular gratitude to Dr Joséphine Th. Koster for her extensive assistance regarding this difficult investigation as well as to Dr R. A. Maas Geesteranus and Dr S. J. van Ooststroom for giving some nomenclatural advice. In the text most literature references are abbreviated; for full titles the bibliography at the end of the paper should be consulted.

* According to the Director of the Staatl. Mus. f. Naturk. u. Vorgesch., Oldenburg, Germany (in a letter to the Rijksherbarium, Leiden, 15 May 1951) the herbarium Roth has been moved from this museum to the Botanical Museum, Berlin, where it was destroyed during the war, 1940-1945.

ON THE DELIMITATION OF *CERAMUM DIAPHANUM* (LIGHTF.) ROTH

In the author's opinion the following species are synonyms of *Ceramium diaphanum*: *Conferva diaphana* Lightf.; *Hormoceras polyceras* Kütz.; *H. nodosum* Kütz.; *H. pulchellum* Kütz.; *H. catenula* Kütz.; *H. cateniforme* Kütz.; *H. moniliforme* Kütz.; *Gongroceras macrogonium* Kütz.; *G. pellucidum* Kütz.; *Ceramium strictum* H. Petersen; *C. vertebrale* H. Petersen and *C. corticatum* Kylin.

However, *C. cimbricum* H. Petersen (Fig. 9), brought to *C. strictum* (Kütz.) auct. f. *stricto-tenuissimum* (H. Petersen) by Sjöstedt (1928), does not belong to *C. diaphanum*. *C. cimbricum* seems to be a good species because of the very slight cortication and the small number of pericentral cells, being 4-5 in the said species and 6-8 in *C. diaphanum*. Beside the type material the author had at his disposal some specimens, washed ashore near Katwijk (Netherlands) attached to a bunch of cork, 17th November 1950, Lucas 888 (L.). Most probably they originate from the Channel.

Ceramium strictum (Kütz.) Harv. is based on *Gongroceras strictum* Kütz. The type of this species appears to belong to *Ceramium deslongchampsii* Chauv., so *C. strictum* Kütz.) Harv. is a synonym of *Ceramium deslongchampsii* Chauv. Moreover ROTH (1806) had already previously described a species *Ceramium strictum* which has been brought to *Hutchinsia* by Lyngbye. According to De Toni *Hutchinsia stricta* (Roth) Lyngb. is a synonym of *Polysiphonia urceolata* (Lightf.) Grev. Since it is impossible to examine the type specimen this question can not be settled. From ROTH's description one gets the impression that his *C. strictum* is not the same species as *C. diaphanum*.

THE DIFFERENTIAL CHARACTERS

A. The series var. *diaphanum* (Lightf.) Roth — var. *zostericola* (Thur.) Feldm. Maz. — var. *tenuissimum* Roth.

In this series the thickness of the thallus-base decreases gradually from about 250-600 μ in var. *diaphanum* and about 170-300 μ in var. *zostericola* to about 100-200 μ in var. *tenuissimum* and at the same time the height of the corticated zones decreases from about 180-600 μ via about 75-170 μ to about 50-120 μ , whereas the length of the hyaline internodes increases from about 1-4 times via about 1-6 times to 1-10 times the width. The number of lateral ramuli is great in var. *diaphanum* (except f. *modificatum* H. Petersen and f. *corticatum* (Kylin) Kylin), small or none in var. *zostericola* and var. *tenuissimum*. The tetrasporangia are not or only slightly projecting in var. *diaphanum*, faintly so (in rare cases much) in var. *zostericola*, and considerably so in var. *tenuissimum*.

H. PETERSEN, H. KYLIN, L. KOLDERUP ROSENINGE, L. G. SJÖSTEDT, T. LEVRING and A. C. J. VAN GOOR consider the possession of gland-cells to be a good discriminating feature of the var. *tenuissimum* Roth. However, they noticed that the number of these cells vary a great deal and may be very small. Mrs. G. FELDMANN-MAZOYER (1940) does not consider this feature a good one. She observed gland-cells in young specimens of var. *diaphanum*. The author saw a fruiting

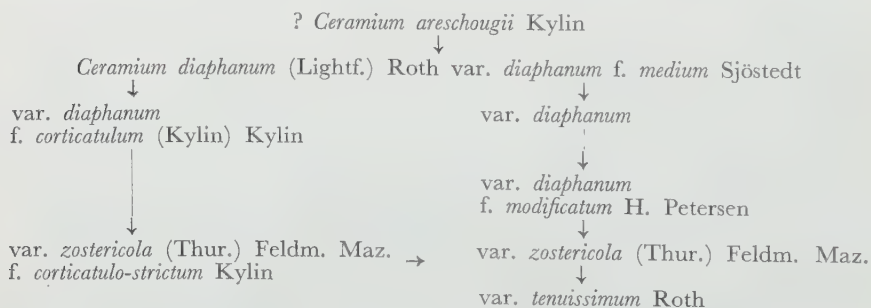
specimen of this variety with some scattered gland-cells and therefore agrees with Mrs. FELDMANN-MAZOYER. The gland-cells are scarce in adult specimens of var. *diaphanum*, but they are more frequent in var. *zostericola* and var. *tenuissimum*, where their number is sometimes so great that they are situated in two whorls.

Another feature of var. *tenuissimum* mentioned by PETERSEN and KYLIN is the possession of dentate apices. These are mostly formed by gland-cells, though sometimes by ordinary cells (this may also be the case when gland-cells exist in the same specimen). They are found in var. *diaphanum* and var. *zostericola*, and especially in var. *tenuissimum*, being most frequent where the apices are more or less incurved. In var. *zostericola* the apices are less often incurved than in the other varieties and consequently they are less often dentate. Dentate apices are to be found in other species as well (e.g.: *C. deslongchampsii* Chauv.).

B. Var. *diaphanum* and forma *medium* Sjöstedt; forma *modificatum* H. Petersen and forma *corticatulum* (Kylin) Kylin; var. *zostericola* (Thur.) Feldm. Maz. and forma *corticatulo-strictum* Kylin.

Forma *medium*, f. *corticatulum* and f. *corticatulo-strictum* differ from var. *diaphanum*, f. *modificatum* and var. *zostericola* respectively in that the cortex in the basal part of the plants proliferate upwards. This proliferation is mostly rather extensive, sometimes even reaching the next corticated zone (vide KYLIN 1909); sometimes it is less extensive. In this way var. *diaphanum* (and possibly also f. *modificatum* and var. *zostericola*) are connected with species entirely corticated in the lower parts of the thallus, such as *C. areschougii* Kylin and *C. fruticosum* (Kütz.) J. Ag.¹ It is remarkable that the Netherlands specimens of var. *diaphanum* are only about 250–370 μ in diam. at the base, whereas f. *medium* is about 350–520 μ in diam. at the base. This also makes the author believe that f. *medium* is intermediate between var. *diaphanum* and the species entirely corticate at the base².

C. These conjectures result in the following scheme:



¹ ROTH (Cat. Bot. Fasc. 2, 1800, p. 183) described a *Ceramium fruticosum*. Judging from the description it is not the same species as *Ceramium fruticosum* (Kütz.) J. Ag., so the latter epithet is invalidated. At present the author is not in the position to carry out an investigation as to this point.

² *Ceramium deslongchampsii* Chauv., which is related to *Ceramium diaphanum* (Lightf.) Roth, probably shows a similar series of forms as the last named species. In *Ceramium deslongchampsii* also the number of lateral ramuli varies from none to numerous, and the development of the cortication varies as well. Material has been

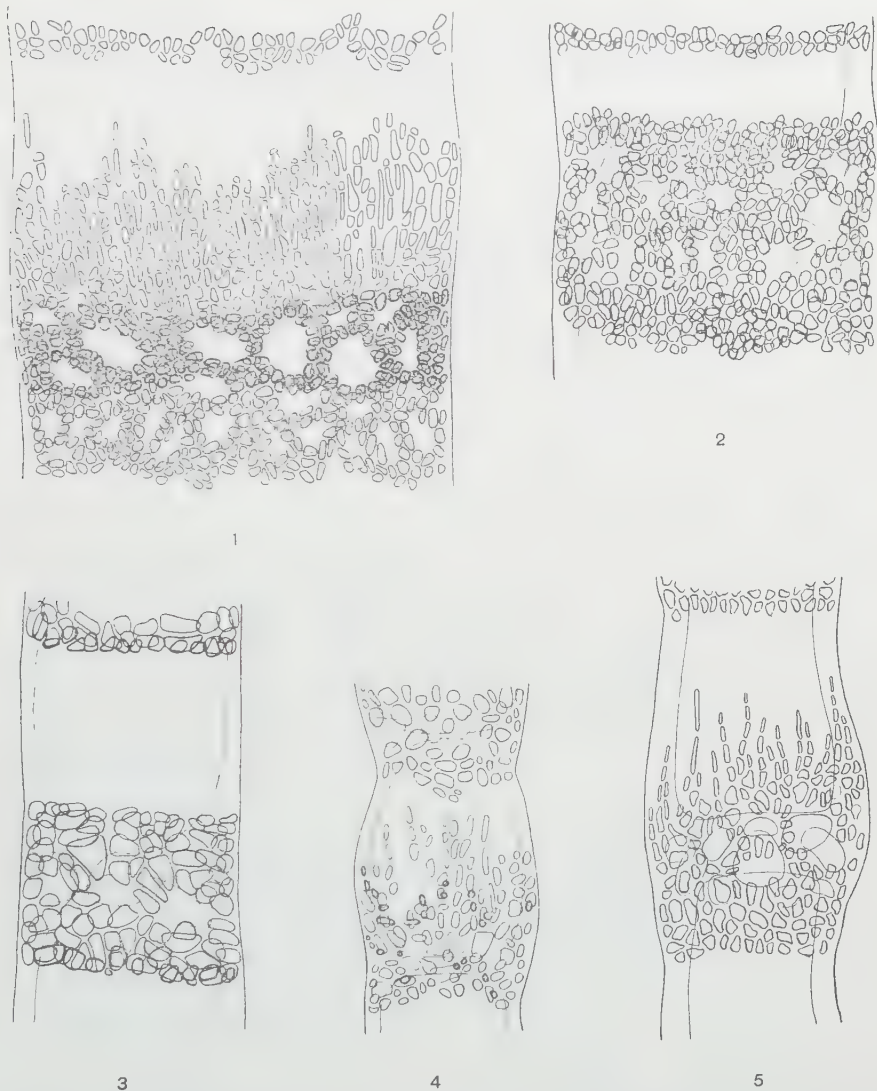


Fig. 1. *Ceramium diaphanum* (Lightf.) Roth f. *medium* Sjöstedt; 2. *C. diaphanum* (Lightf.) Roth var. *diaphanum*; 3. *C. diaphanum* (Lightf.) Roth var. *zostericola* (Thur.) Feldm. Maz.; 4. *C. diaphanum* (Lightf.) Roth var. *zostericola* (Thur.) Feldm. Maz. f. *corticatulo-strictum* Kylin; 5. *C. deslongchampsii* Chauv. f. *semi-ascendens* J. Lucas, f. nov.

found with proliferous cortication. It seems to be reasonable to regard these specimens as belonging to a separate form, of which the description is given below.

Ceramium deslongchampsii Chauv. f. *SEMI-ASCENDENS* J. Lucas, nov. forma (Fig. 5) — articularum inferiorum cellulis corticis ascenditibus, sed genicula superiora confinia non attingentibus.

Type specimen: Den Helder, harbour, 12-4-1950, Swennen and Lucas 281 (L.). This form has also been found on the sea dike at Den Helder, 2-9-1948, Swennen 16 (L.).

THE SPECIES, ITS VARIETIES AND FORMS

Ceramium diaphanum (Lightf.) Roth., Cat. Bot. Fasc. 3, 1806, p. 154. Thallus partly corticated. Corticated zones sometimes proliferating, never entirely covering the internodes. Number of articulations between two main ramifications mostly between 5 and 14, sometimes, especially at the apices much more numerous (e.g. *C. vertebrale* H. Petersen). Pericentral cells mostly 7, covered by 1-4 corticating layers. In young specimens gland-cells among the corticating cells, which afterwards may disappear. Thallus pink, red or more or less brownish, sometimes slightly purplish, but different from the colour in *C. deslongchampsii* Chauv. from which *C. diaphanum* also differs in being more flaccid. Thallus at the base about 100-650 μ in diameter.

Var. *diaphanum* — *Conferva diaphana* Lightf., Flora Scotica, 1777, p. 996, n. 24 —? *Hormoceras moniliforme* Kütz., 1841, p. 733; *H. polyceras* Kütz., 1841, p. 732; *H. polyceras* Kütz. β *majus* Kütz., 1841, p. 732; *H. diaphanum* Kütz., 1841, p. 733; *Gongroceras pellucidum* Kütz. p.p., 1841, p. 735 — Fig. 2.

Thallus at the base about 250-600 μ in diam., in the Netherlands material only 250-370 μ (mostly about 280 μ) in diam., at the apices about 75-120 μ in diam. Corticated zones usually as high as broad or a little shorter, sometimes longer. Corticating layers (outside the pericentral cells) 3 or 4; corticating cells not arranged in longitudinal series. Cells of the outer layer at the base of the zones about 10-30 μ , mostly 15 μ , in diam., those of the upper part of the zones sometimes slightly smaller. Gland-cells mostly disappearing later on. Internodes 1-4 times as long as broad, ecorticated. Apices often incurved, sometimes dentate. Number of lateral ramuli mostly great. Tetrasporangia immersed in the thallus.

On inquiry, the type specimen could be found neither in the British Museum nor in the Herbarium of the Royal Botanic Gardens at Kew nor in that of the Royal Botanic Garden at Edinburgh. The type specimen of *Hormoceras moniliforme* Kütz. is not present in the "Rijks-herbarium" at Leiden. Other specimens, brought to *H. moniliforme* by Kützling, belong to var. *diaphanum*. As to *Gongroceras pellucidum* Kütz., specimens from Trieste as well as from Spalato are present in the collection of the "Rijks-herbarium". The specimens from Spalato have to be brought to var. *tenuissimum*, those from Trieste belong to var. *diaphanum*.

Localities: Monnikendam, 25-7-1905, uncertain whether or not autochthonic there (N.D.V.); Stompe (N.D.V.), the specimen was brought to *C. strictum* Grev. et Harv. by van Goor; Den Helder, harbour, before 1917, on a lighter (N.D.V.); ibid., 15-8-1919, on drifting *Zostera* (N.D.V.); Den Helder, sea-dike, 27-8-1948, Swennen 83 (L.), washed ashore on a bunch of cork; IJmuiden, 19-12-1949, Mulder 38 (L.), washed ashore on a bunch of cork; Bloemendaal, 13-11-1949, Stock 20 and Hazevoet (L.), washed ashore on cork; Zandvoort-Noordwijk, 26-11-1949, Stock 21 (L.), washed ashore on wood; Noordwijkerhout-Noordwijk, 20-1-1949, Lucas 88 (L.), washed ashore on a bunch of cork; Katwijk, 20-11-1950, Lucas 895 (L.), washed ashore on cork; Scheveningen, Vrijdag Zijnen 2 (L.), washed ashore.

f. *modificatum* H. Petersen, Danske Arter af Slaegten Ceramium

(Roth) Lyngbye — D. Kgl. Danske Vidensk. Selsk. Skrifter, 7. Række, Naturvidensk. og Mathem. Afd. V. 2, 1908; p. 60 — *Gonogroceras macrogonium* Kütz., 1862, p. 26 — *Ceranium diaphanum* (Lightf.) Roth f. *strictoides* H. Petersen, 1908, p. 59 — Fig. 11.

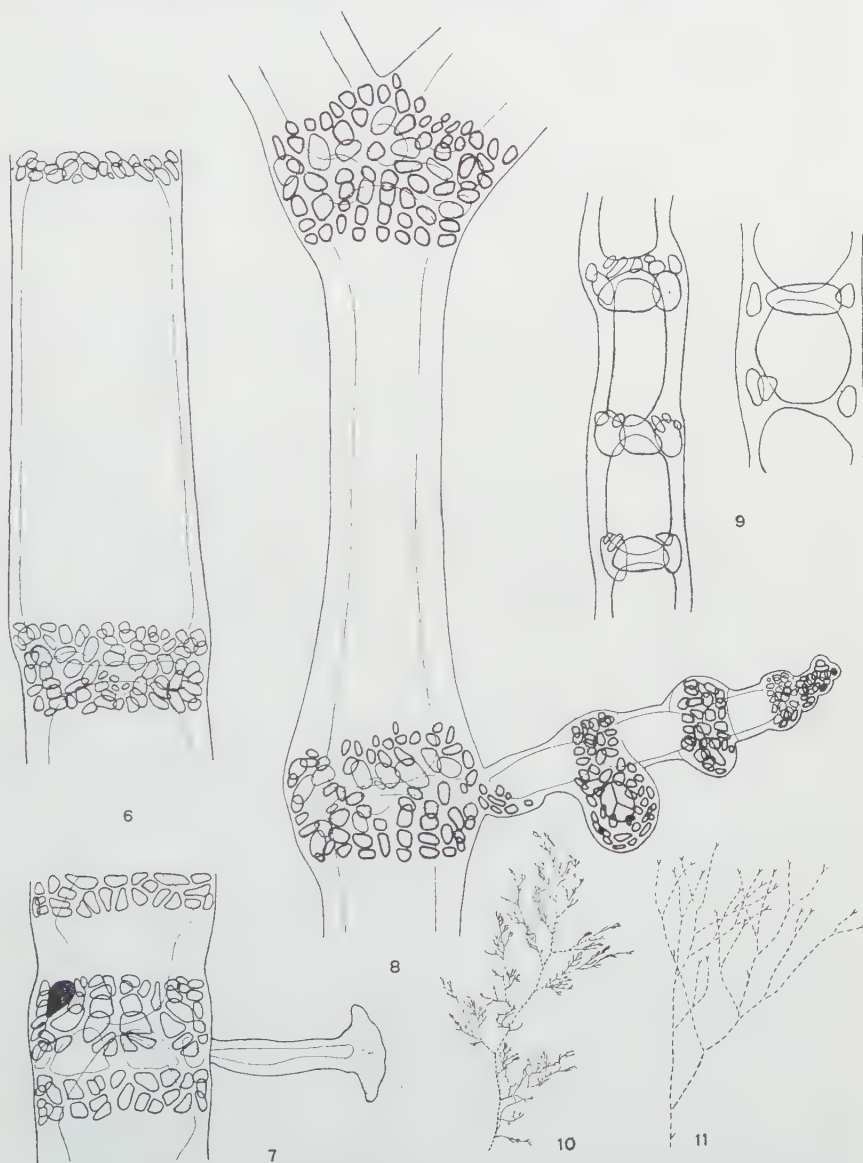


Fig. 6–8. *Ceranium diaphanum* (Lightf.) Roth var. *tenuissimum* Roth: 7. with gland-cell and rhizoid originating from hyaline space, 8. with gland-cells and corticating cells arranged in longitudinal series; 9. *C. cimbricum* H. Petersen, left fig. with more developed cortex; 10. *C. diaphanum* (Lightf.) Roth f. *medium* Sjöstedt, nat. size; 11. *C. diaphanum* (Lightf.) Roth f. *modificatum* H. Petersen, nat. size.

This form is characterized by the lateral ramuli being absent or nearly so.

The present author has examined both the type material of *f. modificatum* H. Petersen and *f. strictoides* H. Petersen. The two forms differ in the height of the corticate zones, which are about equalling the diameter in *f. modificatum*, being shorter in *f. strictoides*. In the author's opinion not only the height of the corticated zones is important for separating var. *diaphanum* and var. *zostericola*, but also the reduction of the thallus as a whole, as is described on p. 323. Accordingly *f. strictoides* has to be considered a synonym of *f. modificatum*.

Localities: Stompe, 9-9-1915, van Goor, in field of *Zostera* (N.D.V.); Den Helder, 15-11-1909, Stomps (A.), on floating *Zostera*; IJmuiden, 19-12-1949, Mulder 40 (L.), washed ashore on a bunch of cork.

f. medium Sjöstedt, Revision of some dubious Swedish *Ceramium* types, their classification and ecology — Lunds Univ. Arsskrift, N.F. Avd. 2. Band 23. Nr. 12, 1928, p. 7 — *Hormoceras cateniforme* Kütz., 1849, p. 675 — *Ceramium diaphanum* (Lightf.) Roth *f. cateniforme* (Kütz.) J. Lucas, 1950, p. 537 — Fig. 5 and 10.

This form is characterized by the corticated zones in the lower part of the thallus showing an upward proliferation by means of elongated cells. However, the next corticated zone is not reached. There is no proliferation in the lowermost corticated zones. The degree of the proliferation is variable, both regarding the density of the cells and the length of the internode that is covered. Sometimes the layer of elongated cells is covered by a second one. When the corticated zone shows proliferation, the outer layer of the zone is mostly looser, especially in the upper part of the zone, and the cells of this layer are more or less elongated.

In the type of this form the proliferation is only slight. In the Dutch material the diameter at the base of the thallus is much larger than in var. *diaphanum*, viz. 350–520 μ (mostly 450 μ). The type specimen of *Hormoceras cateniforme* is even 650 μ in diam. Sometimes the cells of the proliferous layer are not elongated, but more or less angular like the ordinary cells (Lucas 530 and 896). Sometimes it is not in the lower part that the thallus shows proliferation of the corticated zones, but only in the middle parts.

Localities: Only found transported to the Netherlands coast. Texel, 7-10-1946, Bloklander (L.), washed ashore on a bunch of cork; Den Helder, 24-11-1948, Swennen 11 (L.), washed ashore on *Himanthalia elongata*; IJmuiden-Bloemendaal, 19-12-1949, Mulder 39 (L.), washed ashore on *Halidrys siliquosa*; Post 63, 21-9-1950, Mulder 76 (L.), washed ashore on wood; Bloemendaal, 13-11-1949, Stock 18 and 19 and Hazevoet (L.), washed ashore; Post 67-72, 23-9-1950, Mulder 79 (L.), washed ashore on *Himanthalia elongata*; Noordwijkerhout-Noordwijk, 24-10-1948, Lucas 8 (L.), washed ashore on wood; *ibid.*, 20-1-1949, Lucas 4 (L.), washed ashore on cork; Noordwijk, 24-10-1948, Lucas 66 and 67 (L.), washed ashore on a board; Katwijk, 15-10-1938, Lacourt (L.), washed ashore on a bunch of cork; *ibid.*, 18-12-1949, Lucas 530 (L.), washed ashore on *Aglaophenia pluma*; Post 85-86, 20-11-1950, Lucas 896 and 900 (L.), washed ashore on cork; Wassenaarse Slag-Scheveningen, 30-11-1947, Lucas 48 and 285 (L.), washed ashore on *Ascophyllum nodosum*; Post 95-96, 19-9-1946, Leenhouts 145 (L.), washed ashore on a bunch of cork.

f. *corticatulum* (Kylin) Kylin, Svensk Bot. Tidskr. Bd. 3, H. 3, 1909, p. 330 — *Ceramium corticatum* Kylin, 1907, p. 176.

This form is characterized in that the lateral ramuli are wanting or nearly so and moreover in that the proliferation of the corticated zones in the lower parts is as in f. *medium* Sjöstedt. KYLIN himself (1909) regarded *Ceramium corticatum* as a form of *Ceramium diaphanum* (though in his later papers he again considers it a separate species), so the new combination, *Ceramium diaphanum* (Lightf.) Roth f. *corticatum* (Kylin) Sjöstedt (1928), was superfluous.

The type specimen measures 350 μ in diameter at the base.

Locality: Wassenaarse Slag-Scheveningen, 30-11-1947, Lucas 289 (L.), washed ashore on *Ascorphyllum nodosum*.

Var. *zostericola* (Thur.) Feldm. Maz., Recherches sur les Ceramiales de la Méditerranée occidentale. 1940, p. 314 — *Ceramium strictum* Harv. var. *zostericola* Thur., Algues marines de Cherbourg no 123; *C. strictum* auct. non Roth nec (Kütz.) Harv.; *Hormoceras catenula* Kütz., 1847, p. 35; ? *H. pulchellum* Kütz., 1849, p. 676; *Ceramium strictum* H. Petersen f. *vera* p.p., 1908, p. 62; *C. vertebrale* H. Petersen, 1908, p. 63 — Fig. 3.

Thallus at the base about 170–300 μ in diam. (mostly about 230 μ) at the apices about 40–75 μ . Height of the corticated zones less than the width. Corticating layers (outside the pericentral cells) 2 or 3, corticating cells not arranged in longitudinal series. Cells of the outer layer at the base of the corticate zones about 9–25 μ in diam., in the Netherlands specimens mostly 10–12 μ , those of the upper part of the zones often slightly smaller. Gland-cells are often found among the corticating cells, sometimes being arranged in a whorl. Length of the internodes 1–6 times the width, internodes ecorticated. Apices often straight, rarely dentate. Number of lateral ramuli small. Tetrasporangia more or less projecting.

As the ramification in *Ceramium diaphanum* varies a great deal, it seems useless to separate a form with fasciculate branches from var. *zostericola*. Both types of ramification have been found in the Netherlands.

KYLIN, SJÖSTEDT and KOLDERUP ROSENVINGE consider the fact that the height of the corticated zones is less than the width a specific character of this variety. However, though this feature is found in very thick specimens (up to about 550 μ), other specimens, measuring only 170 μ in diam. at the base, have corticated zones in which the height equals the width. Therefore this feature does not seem of much value, and the author agrees with Petersen, who separates f. *strictoides* H. Petersen and *C. strictum* H. Petersen (non Roth). In his opinion it is the reduction of the thallus as a whole which seems a better criterion for separating this variety.

The type specimen of *Hormoceras pulchellum* Kütz. is not present in the "Rijksherbarium" at Leiden. A specimen identified by Kützling as this species belongs to var. *zostericola*. In rare cases the corticated zones are divided into two parts by a horizontal hyaline space.

Localities: Steile Bank, 15-7-1905 (N.D.V.); Den Helder, 3-8-1930, Sobels

(U.), on drifting *Zostera*; Huisduinen, 9-10-1948, Swennen 10 (L.), washed ashore on Fucus; Noordwijk-Katwijk, 15-11-1949, Lucas 511 (L.), washed ashore on *Halidrys siliquosa*; Post 85-86, 20-11-1950, Lucas 885 (L.), washed ashore on cork; Scheveningen, 17-9-1941, Creutzberg (L.), washed ashore on Fucus; Kijkduin, 20-11-1949, Lems (L.), washed ashore on a beam.

Of the material, collected by VAN GOOR (1923), only one specimen is left; it originates from Stompe. This specimen, however, belongs to var. *diaphanum*.

f. *corticatulo-strictum* Kylin, Svensk Bot. Tidskr. Bd. 3, H. 3, 1909, p. 332. Fig. 4¹.

Differs from var. *zostericola* by the upward proliferation of the nodal cells in the lower parts of the thallus. In the proliferous zone we find elongated cells. According to KYLIN in rare cases the next corticated zone may be reached. The lowermost zones do not show proliferation. The degree of the proliferation is variable as to the density of the cells as well as to the length of the internode that is covered. In the specimens examined the outer layer consists of very few angular cells only, separate or arranged in scattered groups.

KYLIN includes in this form also those specimens of f. *corticatulum*, in which the height of the corticated zone without the proliferous part is less than the width. As stated above this feature seems to be of no special value. The type specimen of f. *corticatulo-strictum* was not available.

Localities: Zuiderzee at Durgerdam, 4-1882, Weber (L.); Noordwijk-Katwijk, 15-11-1949, Lucas 487 (L.), washed ashore on a bunch of cork.

Var. *tenuissimum* Roth, Cat. Bot. Fasc. 3, 1806, p. 156 — *Hormoceras nodosum* Kütz., 1841, p. 732; *H. pellucidum* Kütz. p.p., 1841, p. 735 (vide sub var. *diaphanum*); *Ceramium diaphanum* (Lightf.) Roth f. *stricto-tenuissimum* H. Petersen, 1908, p. 62; *C. strictum* H. Petersen f. *verum* p.p., 1908, p. 62 — Fig. 6-8.

Thallus at the base about 110-200 μ in diam., mostly 130-140 μ , at the apices about 40-75(-100) μ . Height of the corticate zones mostly less than the width, very variable. Corticating layers (outside the pericentral cells) 1 or 2; corticating cells irregularly arranged or more or less in longitudinal series, especially in the lower part of the zone. Cells of the outer layer at the base of the zones 9-18 μ , (mostly 15 μ) in diam., those of the upper part of the zones mostly smaller. Gland-cells are often found among the corticating cells, sometimes arranged in 1 or 2 whorls. Length of the internodes 1-10 times the diameter, internodes ecorticated. Apices often incurved, dentate or entire. Number of lateral ramuli small. Tetrasporagia strongly projecting, at the outer side of the zones or in whorls.

As stated above neither the presence of gland-cells nor that of dentate apices is a good criterion for this variety. Mrs. G. FELDMANN-MAZOYER, 1940, p. 300 indicates another feature, viz. the arrange-

¹ In M. WAERN, Rocky-shore Algae in the Öregrund Archipelago — Acta Phytogeogr. Suec., 30, 1952, p. 207, a paper which appeared after the present one was finished, *C. diaphanum* (Lightf.) Roth f. *corticatulo-strictum* Kylin is brought to the synonymy of *C. tenuicorne* (Kütz.) Waern, together with *C. vertebrale* H. Petersen.

ment of the corticating cells in longitudinal series. She herself admits that these series are not always distinct. Among the material studied by the author there are some in which the corticating cells are only indistinctly arranged in longitudinal series. One specimen (*Lucas 13*) shows longitudinal series in the greater part of the corticated zones, whereas in the remaining part the cells are irregularly arranged. Therefore var. *tenuissimum* Roth sensu G. Feldm. Maz. cannot be considered a separate species.

Often a horizontal hyaline space divides the corticated zone into two parts, viz. a narrow lower part and a broader upper one. The corticating cells are arranged more or less in longitudinal series, especially in the lower part. From this space rhizoids may originate, sometimes being arranged in whorls.

Localities: Texel, 17-11-1884, Weber-van Bosse (L.); ibid., 7-10-1946, Bloklander (L.), washed ashore on a bunch of cork; Hoorn, 9-1854, Suringar 148 (L.), on Nematium; De Balg, 6-1886, Weber-van Bosse (L.); Den Helder, Zuidwal, 9-12-1915, van Goor (N.D.V.); Den Helder, Vangdam, on drifting *Zostera* (N.D.V.); Nieuwediep, 7-1887, Weber-van Bosse (L.); IJmuiden, 19-12-1949, Mulder 41 (L.), washed ashore on a bunch of cork; Post 56-63, 21-9-1950, Mulder 85 (L.), washed ashore on *Ascophyllum nodosum*; Zandvoort, 10-1845, Buse (L.), washed ashore on *Chorda filum*; Noordwijkerhout-Noordwijk, 20-9-1948, Lucas 13 (L.), washed ashore on *Chorda filum*; ibid., 24-10-1948, Lucas 537 (L.), washed ashore on *Ascophyllum nodosum*; Noordwijk-Katwijk, 15-11-1949, Lucas 482 (L.), washed ashore on a bunch of cork; ibid., 15-11-1949, Lucas 512 (L.), washed ashore on *Ascophyllum nodosum*; ibid., 15-11-1949, Lucas 513 (L.), washed ashore on *Fucus vesiculosus*; ibid., 15-11-1949, Lucas 514 (L.), washed ashore on *Ascophyllum nodosum*; Katwijk, 29-9-1950, Lucas 818 (L.), washed ashore on *Fucus vesiculosus*.

REFERENCES

- FELDMANN-MAZOYER, G., Recherches sur les Ceramiacées de la Méditerranée occidentale. Alger. 1940.
 Flora Danica, Tab. 951. 1792.
 FOSLIE, M., The Norwegian Forms of *Ceramium* — Det. Kgl. norske Videnskabers Selskabs Skrifter, Trondhjem, 1-21. 1893.
 GOOR, A. C. J. VAN, Die Holländischen Meeresalgen — Verh. Kon. Akad. Wetensch. Amsterdam, 2e Sect. Dl. XXIII, No. 2. 1923.
 HARVEY, W. H., Phycologica Britannica. London. 1846-1851.
 HAUCK, F., Die Meeresalgen Deutschlands und Oesterreichs — Rabenhorst Kryptogamenflora, Bd. 2. Leipzig. 1885.
 JOLIS, A. LE, Liste des Algues marines de Cherbourg. 1863.
 KOLDERUP ROSENVINGE, L., The marine algae of Denmark I, Rhodophyceae — D. Kgl. Danske Vidensk. Selsk. Skrifter, 7. Raekke, Naturvidensk. og Mathem. Afd., VII. 1-4. København. 1909-1931.
 KÜTZING, F. T., Ueber *Ceramium* Ag. — Linnæa XV, 727-746. 1841-2.
 KÜTZING, F. T., Diagnosen und Bemerkungen zu neuen oder kritischen Algen — Bot. Zeitung, V, 35. 1847.
 KÜTZING, F. T., Species Algarum. Lipsiae. 1849.
 KÜTZING, F. T., Tabulae Phycologicae, Bd XII. 1862.
 KYLIN, H., Studien über die Algenflora der schwedischen Westküste. Akademische Abhandlung. Uppsala. 1907.
 KYLIN, H., Studier öfver Några Svenska *Ceramium* Former — Svensk Bot. Tidskr. Bd 3, H. 3, 330-332. 1909.
 KYLIN, H., Bemerkungen über einige *Ceramium* Arten — Botaniska Notiser 1924, 443-452. Lund. 1924.

- KYLIN, H., Die Rhodophyceen der Schwedischen Westküste — Lunds Univ. Årsskrift. N.F.Avd. 2. Bd. 40. Nr. 2. Lund. 1944.
- LAKOWITZ, K., Die Algenflora der gesammten Ostsee. Dantzig. 1929.
- LEVING, T., Zur Kenntniss der Algenflora der Norwegischen Westküste — Lunds Univ. Årsskrift. N.F.Avd. 2. Bd 33, Nr 8. Lund. 1937.
- LIGHTFOOT, Flora Scotica, Vol. 2, n. 24, 996. 1777.
- LUCAS, J. A. W., The Algae transported on drifting objects and washed ashore on the Netherlands Coast — Blumea, VI, no 2, 536–537. 1950.
- LYNGBYE, H. C., Tentamen Hydrophytologiae Danicae. 1819.
- NEWTON, L., A Handbook of the British Seaweeds. London. 1931.
- PETERSEN, H. E., Danske Arter af Slægten Ceramium (Roth) Lyngbye — D. Kgl. Danske Vidensk. Selsk. Skrifter, 7. Raekke, Naturvidensk. og Mathem. Afd. V. 2. København. 1908.
- PETERSEN, H. E., Ceramium Studies, Bot. Tidskr. 31. 1911.
- Prodromus Florae Batavae, Vol. II, pars II. 1853.
- SJÖSTEDT, L. G., Undersökningar öfver Oeresund, XIV — Revision of some dubious Swedish Ceramium types, their classification and ecology — Lunds Univ. Årsskrift, N.F.Avd. 2. Bd 23. Nr 12. Lund. 1928.
- ROTH, A. W., Catalecta Botanica, Fasc. II, 1800; Fasc. III. 1806.
- TAYLOR, W. R., Marine Algae of the Northeastern Coast of North America — University of Michigan studies, Vol. XIII, Norwood. 1937.
- TONI, G. B. DE, Sylloge Algarum omnium hucusque cognitarum. Padua, (1889–1924).

STARCH CONVERSION IN LEAVES OF HELIANTHUS TUBEROSUS AND H. ANNUUS: PRELIMINARY OBSERVATIONS

BY

E. C. WASSINK

*Laboratory of Plant Physiological Research, Agricultural University,
Wageningen, Netherlands; 111th Communication**

(Received March 27th, 1953)

1. INTRODUCTION

The knowledge of the biochemistry of carbohydrate conversion has strongly increased in the last decenniae (*cf.*, *e.g.*, 1). It seems that the development has been less strong in the field of the biology of carbohydrate conversion. In this statement it is understood that the study of the biochemistry of carbohydrate conversion is concerned with the pathways of these conversions and the enzymes involved. On the other hand, the study of the biology of carbohydrate conversion is concerned with the conditions under which these conversions take place in plant material.

The present paper is restricted to reporting some preliminary observations on starch conversion in leaves, especially in relation to leaf temperature.

The problem of starch conversion in leaves has several points of interest, a few of which may be mentioned. It can be looked upon as one of the major initial steps in the translocation of organic material, built up by photosynthesis. As such it probably counteracts some final steps of the photosynthetic chain (*i.e.*, the formation of starch) but, on the other hand, in the absence of any dissolution and translocation of starch, photosynthesis might come to a stand still. As to these questions, not much more than rather vague information exists. As will be demonstrated in the present paper — and has been known for a long time — leaves are depleted from starch more or less thoroughly in the dark, dependent on external conditions. It can be supposed that photosynthesis during the next day is more or less connected with the degree of depletion. During darkness, the process of starch conversion can be studied, apart from starch formation by photosynthesis. It may be supposed that starch conversion strongly influences other aspects of the nocturnal metabolism of a leaf. A more

* The author wishes to thank Miss G. DE VOS (now Mrs. G. KERKHOF MOGOT-DE VOS) for manifold assistance.

extensive knowledge of the underlying processes may be important also for the understanding of metabolic mechanisms connected with photoperiodic and thermoperiodic reactions. Starch conversion also may play a role in creating higher osmotic pressures, thus counteracting wilting. It may be mentioned here that, during the present investigation, the incidental observation was made that leaf fragments which, for some reason, had wilted during the experiment, as a rule showed a much stronger hydrolysis of starch than those that had remained turgescient.

The following reasons why our knowledge about the biology of starch conversion in leaves is not yet very complete, may be mentioned.

1. The variation and specialization as to plant species.
2. The rather complex operation required for complete sugar analysis.
3. The variation of individual leaves.

These points suggest the desirability of a simple method, allowing rapid, serial work.

2. MATERIAL AND METHODS

The experimental plants were *Helianthus tuberosus* (a clone, indicated by the name "Violet") and *H. annuus*, grown from seeds. Both were cultivated in the experimental field of this laboratory. Most experiments were made with halves of detached leaves, and with leaf discs. Some experiments were made with leaves attached to stem pieces of about 50 cm length, including the tip of the stem. In some cases, starch conversion was followed in leaves attached to the intact plants in the field. The work was begun in 1948; most of the experiments reported in this paper were made in the late summer and the early autumn of 1950. For the laboratory experiments, the leaves were collected at about sunset. The first series were made with leaf halves. The leaves were cut along the mid rib, the ribless half was used as a blank, and the half with the petiole served as experimental material. For this purpose, the petiole was introduced into a small bottle with water and placed under the conditions of the experiment. Six leaf halves were placed in each condition (*e.g.*, each temperature of a series). At the start of an experiment, the blanks were killed by quickly dipping them into boiling water three times in succession, and collected in glass boxes with 80 % ethanol for chlorophyll extraction. At the end of the experiment, the other leaf halves were treated likewise. The extraction of chlorophyll, including some renewals of ethanol, required about 3 days.

The starch determination was carried out in a very simple manner, briefly as follows. After the chlorophyll had been extracted (the leaves then being yellowish white), the starch was stained by replacing the ethanol by an iodine mixture according to SACHS (2). This mixture contained 10 g J in 1 l. 96 % ethanol, filled up to 2 l. with distilled water. Homogeneous staining was reached satisfactorily by staining the sets of leaf halves (*e.g.* 48 items) in large, glass covered glass boxes on a small shaking machine for some hours, or, eventually, a whole night. Evaporation of the iodine has to be prevented. The leaf halves remained in the staining mixture until the staining intensity was estimated. This estimation was made colorimetrically, using a photronic cell (mark "Megatron"), mounted in a square wooden frame of about 12 × 12 cm, and covered by an orange glass. The transmission curve of this glass was roughly similar to that of SCHOTT's OG 2. The amount of starch in a leaf half, treated as indicated above, was estimated by laying the leaf half as flatly as possible on the orange glass above the sensitive surface of the photronic cell.

The source of illumination was an incandescent bulb of 60 Watt at a distance of about 50 cm. The orange glass was intercalated, in order to increase the contrast between the blueish shade of the starch-rich leaf halves and the yellow color of those poor in starch, and also to decrease the straylight. The photo-electric current was measured with a μ -amp meter; in the range used (up to 20 μ -amp) the deflection was linear in relation to the intensity of illumination of the photocell (fig.1.).

Mostly the measurements were made late in the evening. Then the constancy of the lamp was very good; it was checked many times, using a violet glass as a standard.

In the graphs, the μ -amp values of the transmitted light are given. So, high values indicate little starch, low values much starch. The relation of the μ -amp value to the starch content cannot be assumed to be linear, but a lower transmission will indicate a higher starch content and vice versa. This is easily seen by visual observation also. Considerations concerning BEER's law hardly seem worth while

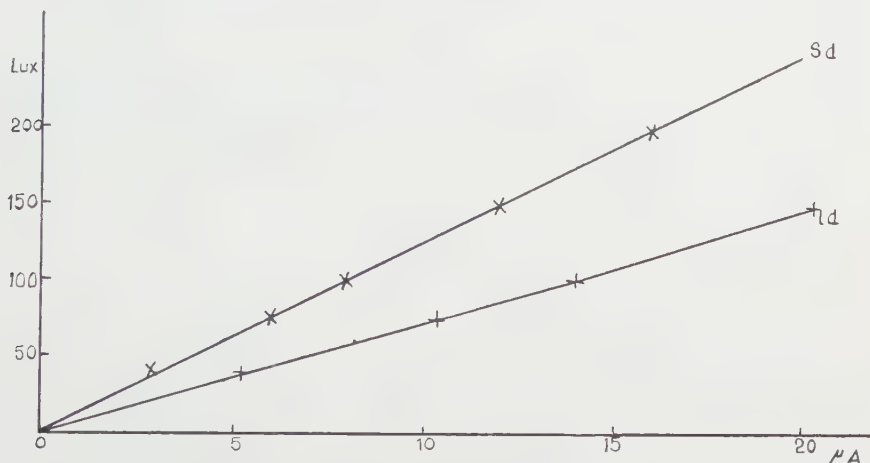


Fig. 1. Calibration of the light transmission meter. Lux values have been applied in special calibration cabinet, used for other calibrations in this laboratory also. sd = small, ld = large diaphragm. With orange glass (see text).

here, since the complicated behavior of the stray light in leaves with strongly different transmission values can hardly be estimated. But, for a preliminary survey, this does not seem necessary.

During the measurements, it was observed that as a rule the distribution of starch in a leaf half was very homogeneous. Therefore, in a further stage of the work, the exposition of half leaves was replaced by exposition of leaf discs of about 30 (in some cases about 25) mm in diameter, taken from the leaves in such a way that the larger ribs were avoided as much as possible. For a temperature series, a disc from each leaf was placed at each temperature; for an experiment 6 leaves were used. Thus, six discs were placed in a petri dish (one from each leaf), and such a dish was exposed at each temperature. The discs were mounted upon a gauze plate, resting upon glass bars with water underneath. At the bottom and inside the cover of the petri dish was moist filter paper.

Also these leaf discs, devoid of their connection with the midrib, showed extensive starch breakdown.

In this way a much more elegant set-up was obtained; an experiment with 6 replicates and 8-12 different conditions required only 6 leaves, and much smaller amounts of iodine than in the case of leaf halves, whereas they remained flat much better than half leaves. The simplicity of handling is especially demonstrated by the remark that, in 1950, in a period of about 6 weeks, near 5000 separate starch estimations have been made.

3. EXPERIMENTAL RESULTS AND THEIR DISCUSSION

a. The course of the starch content of leaves during the daily cycle

Fig. 2 shows observations on the course of the starch content during the daily cycle in leaves of *Helianthus tuberosus* under natural conditions, on October 4, 5 and 6, 1950. The observations were made by taking

samples from six leaves (discs of about 25 mm in diameter) pierced out of the leaves at various moments during day and night, and subsequently treated and measured as described in section 2. In order to interfere the least possible with the health of the remaining part of the leaf, the sampling proceeded from the tip to the bottom, leaving big ribs intact as long as possible. Thus, 18 subsequent samples were taken from each leaf, yielding the curves shown in fig. 2. It is seen that each of the 6 leaves behaves in virtually the same way, and that the average curve gives a good representation. The starch content of the leaves is lowest in the early morning (from about 6–9 h), highest

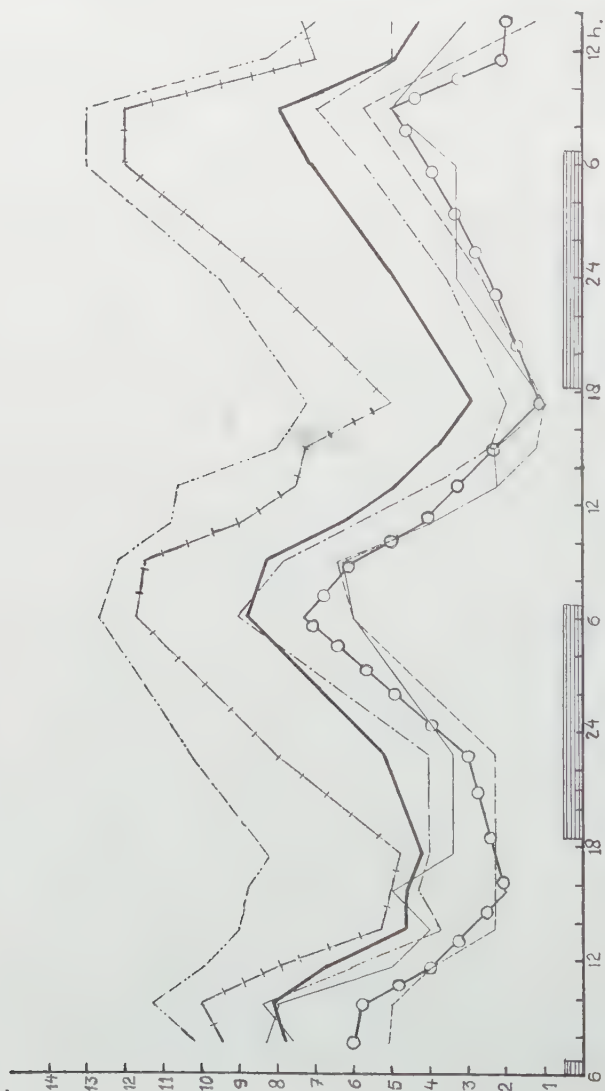


Fig. 2. Daily course of starch content in 6 leaves of *Helianthus tuberosus*. Abscissa: time in hours, shaded parts = night; ordinate: light transmission. Heavy line: average curve. Cf. also text. Exp. of 4, 5 and 6 October 1950.

in the afternoon (between 16 and 18 h). It should be noted that the shape of the curves cannot be evaluated as depletion rate curves or starch formation rate curves, since the numerical relationship between starch content and light transmission is not known. Nevertheless, some curves suggest that starch dissolution in the second part of the night is more effective than in the first few hours of darkness. Table 1 gives some atmospheric data on the days of the observations.

TABLE 1
Some atmospheric data belonging to the observations on starch conversion in leaves of *Helianthus tuberosus* under natural conditions. Exp. of 4-6 October 1950.

Date	Hour	Temp. (°C)	Remarks
1950 4.10	7.30	10.2	—
	11.30	14.8	covered
	13.30	15.6	covered
	15.30	15.9	covered
5.10	6.—	8.5	lightly covered
	9.—	10.0	lightly covered, sun coming through
	11.15	15.0	lightly covered, weak sun
	13.15	18.1	sunny, somewhat hazy
	15.—	18.8	sunny
	17.30	16.0	no sun on the plants any more
	24.—	11.5	clear
6.10	6.—	10.0	clear with light fog
	9.—	13.2	sunny
	11.45	19.0	sunny
	13.45	21.1	sunny
	16.45	19.8	sunny. Only 4 leaves left. Points not in graph.

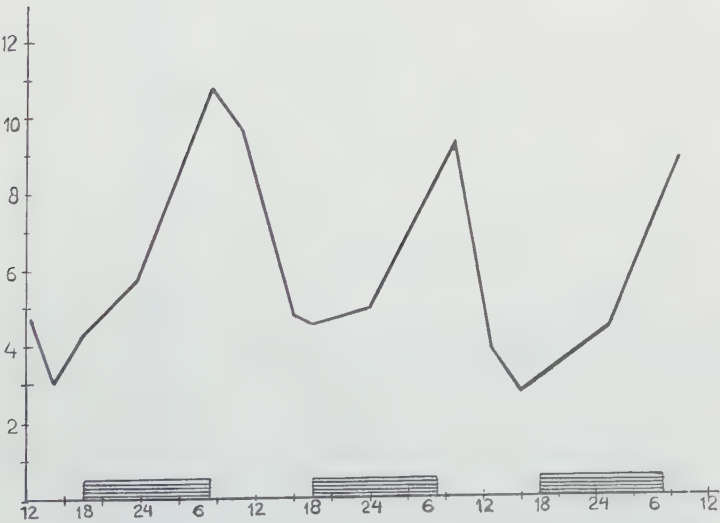


Fig. 3. Same as fig. 2, for *Helianthus annuus*. Average of 4 leaves. Exp. of 13, 14, 15 and 16 October 1950.

Fig. 3 shows a similar curve, taken on October 14–16, 1950 in healthy leaves of *Helianthus annuus*. This curve is an average of 4 leaves. The behavior is the same, even in details, as observed in *H. tuberosus*.

Table 2 gives atmospheric data pertaining to the observations in *H. annuus*. In relation to this experiment, light intensities have been measured along with the collection of leaf samples, with the aid of the spherical radiation meter (cf. 3).

The curves of fig. 2 and 3 do not contain any suggestion that the process of starch metabolism shows conspicuous differences in a short day plant (the race of *H. tuberosus* used) as compared with a plant flowering in long days (*H. annuus*). More observations, however, are needed to judge whether this applies more generally.

b. Starch hydrolysis in relation to temperature

Most of the experiments reported in this paper are concerned with the influence of temperature. The samples were exposed in darkness in thermostates of the temperatures indicated. Either leaf halves with their petioles in small bottles with water, or discs, mounted on gauze in petri dishes (cf. section 2) were used. Mostly 8 temperatures, from 3° to 31° C, sometimes 12 temperatures, between — 3° and 40° C, were used.

Some characteristic curves are shown in figs 4, 5, 6, 7 and 8. Fig. 4

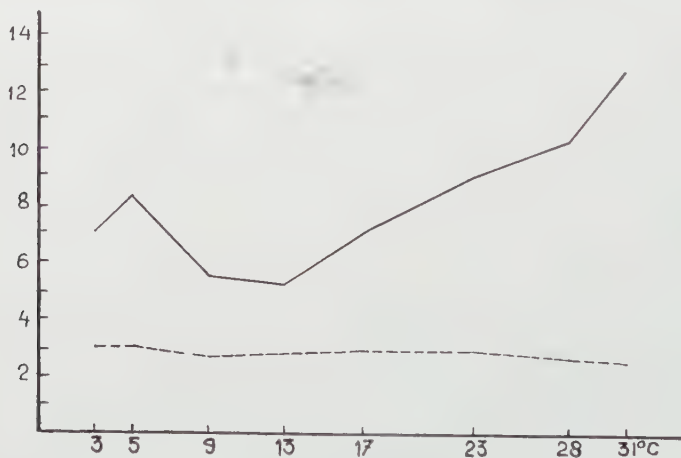


Fig. 4. Starch hydrolysis in relation to temperature. Leaf halves of *Helianthus tuberosus*. Exposition time $6\frac{1}{2}$ hours. Dotted line: Control at the start of experiment. Full drawn line: Light transmission (ordinate) at the end of the experiment. Each point average of 6 leaves. Exp. of 13–14 September 1950.

represents an experiment of relatively short duration ($6\frac{1}{2}$ h) with leaf halves of *H. tuberosus*; fig. 5 shows a similar experiment with leaf discs (≈ 30 mm diam.) of the same species (duration $8\frac{1}{2}$ h) over a more extensive temperature range. Fig. 6 shows a similar experiment, made with smaller leaf discs and over a longer experimental period ($14\frac{1}{2}$ h).

TABLE 2

Some atmospheric data pertaining to the experiment on starch conversion in leaves of *Helianthus annuus* under natural conditions. Light intensities in μ -Watts/cm² cross section, measured with the spherical radiation meter (3). Exp. of 13 16 October 1950

Date		13.10.1950			14.10.1950			15.10.1950			16.10.1950	
Leaf number	Hour	12.15	14.30	17.30	7.30	10.45	13.15	16.00	9.15	13	16.00	8.45
	Light intensity	∞ 60000 ∞ 60000 14500 ∞ 60000	22600 8400* ∞ 60000 ∞ 60000	1240 550 285 260	5200 2400 3250 3050	14500 11300 16200 16700	16000 10200 ∞ 15000 ∞ 15000	12000 7800 8700 9500	15000 5900 9700 9700	38000 18000 24000 16000	13000 9000 10200 10500	3800 2700 3150 3350
	Temp. (° C)	19	20.5	13	8	14	14	12	9	14	14	10.5
	Atmospheric condition	bright sun the whole day			cloudy	cloudy	slightly cloudy	slightly cloudy	foggy	slightly cloudy no direct sun	cloudy	

* leaf shaded

Fig. 7 shows a short duration experiment over a large temperature range with large discs of *H. annuus*; fig. 8 shows a similar experiment with smaller discs over a longer period. In all cases 6 items were averaged for each point.

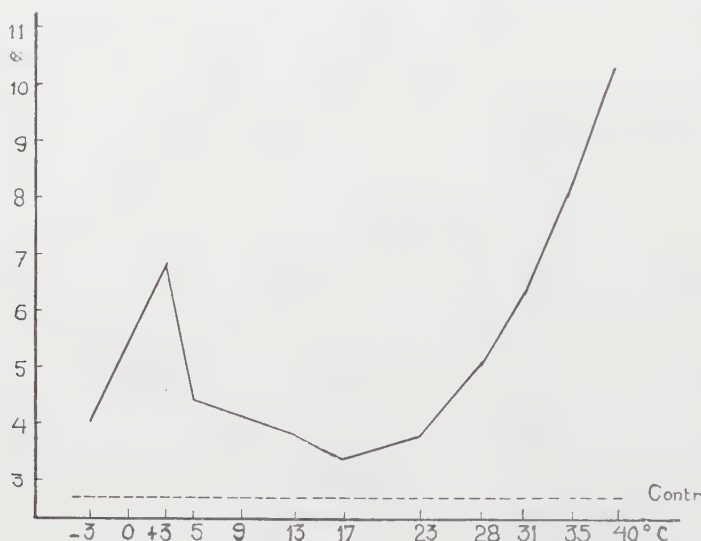


Fig. 5. Starch hydrolysis in relation to temperature. Leaf discs from *Helianthus tuberosus*. Exposition time $6\frac{1}{2}$ hours. Dotted line: control at the start (horizontal line through the average ordinate of 6 discs). Full drawn line: light transmission (ordinate) at the end of experiment. Control, and hydrolysis value at each temperature average of 6 discs, derived from the same set of 6 leaves for all temperatures. Exp. of 9-10 October 1950.

The following features of the curves are obvious. In practically all cases (with the exception of the short duration experiment with *H. annuus* (fig. 7)), starch hydrolysis in relation to temperature shows two maxima separated by a, mostly very pronounced, minimum. In both species the first maximum develops between -3° and $+5^{\circ}$ C, with the highest values probably between 0° (or somewhat below 0°) and $+3^{\circ}$ C. This obviously coincides with the region in which potato tubers turn "sweet". So far, however, I have not attempted a direct comparison of both reactions. Also, the tubers of *Helianthus tuberosus* have not been investigated in this respect, so far. It should be noted that the reaction in the leaves is the same in *H. tuberosus* and *H. annuus*, the latter not forming tubers. The minimum in the hydrolysis curve extends from about 5° to 20° C, the deepest region being situated between 9° and about 15° . From about 15° onward the hydrolysis curve shows a rather rapid increase. In the experiments of short duration, the degree of hydrolysis increases up to the highest temperatures, applied in both species (fig. 5, 7). In the experiments of longer duration, hydrolysis shows about the same (high) values from about 28° onward, probably meaning complete hydrolysis of the starch present. In fig. 8, the 40° C

point is abnormally low; in this case all 6 discs had a blackish necrotic appearance at the end of the experiment. Especially at 17°C , the hydrolysis value, with respect to the minimum values recorded at slightly lower temperatures, is rather sensitive to the duration of the experiment. It should be remarked especially that even at -3°C

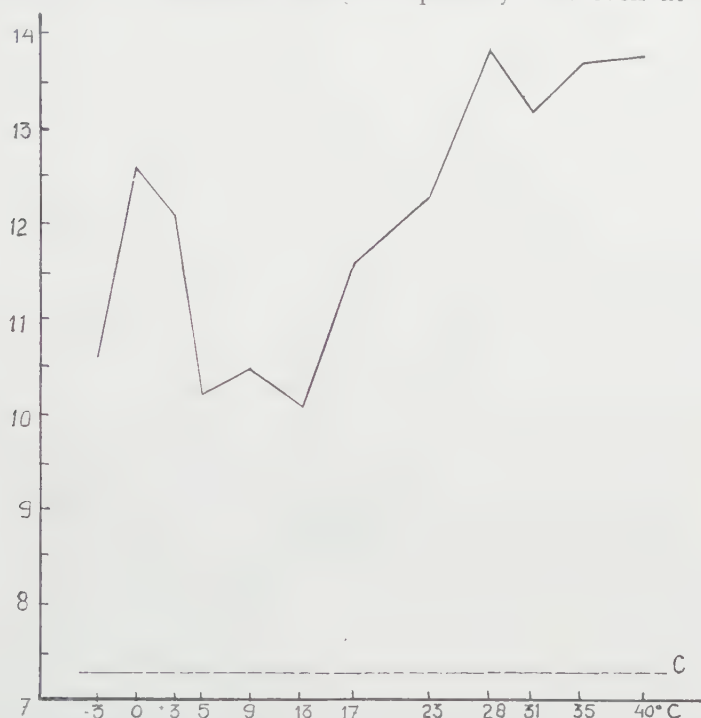


Fig. 6. Starch hydrolysis in extensive temperature range. Leaf discs of *Helianthus tuberosus*. Exposition time $14\frac{1}{2}$ h., 6 leaves. See further: caption of fig. 5. Exp. of 29–30 September 1950.

an appreciable hydrolysis takes place (*cf.*, the corresponding blanks, taken prior to the experimental period from the same leaves). Its value is more or less comparable to that at about $+13^{\circ}\text{C}$.

Some considerations concerning the possible nature of the minimum will be given below.

A further remark to be made is that hydrolysis, as to amount and temperature characteristics, does not show any conspicuous differences whether leaf halves or discs are used. It will be shown presently, that also the connection of the leaves to a stem piece does not make any difference. In all cases hydrolysis can run fairly to completeness in the duration of one night, provided the other conditions are favorable. It seems possible to conclude (provisionally) that in first instance starch hydrolysis is a cellular process which may proceed to completeness irrespective of transport possibilities over long distances.

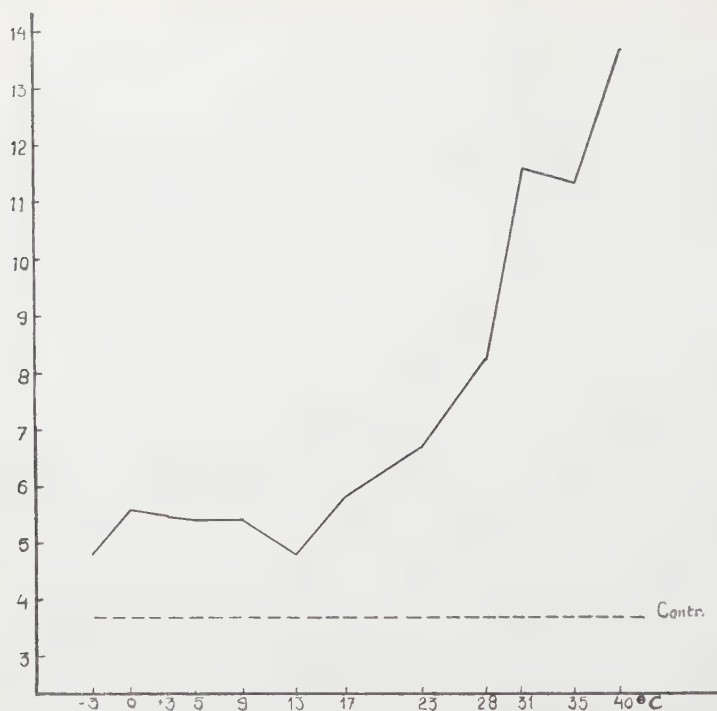


Fig. 7. Starch hydrolysis in extensive temperature range. Leaf discs from *H. annuus*. Exposition time 8½ h., 6 leaves. See further: caption of fig. 5. Exp. of 9-10 October 1950.

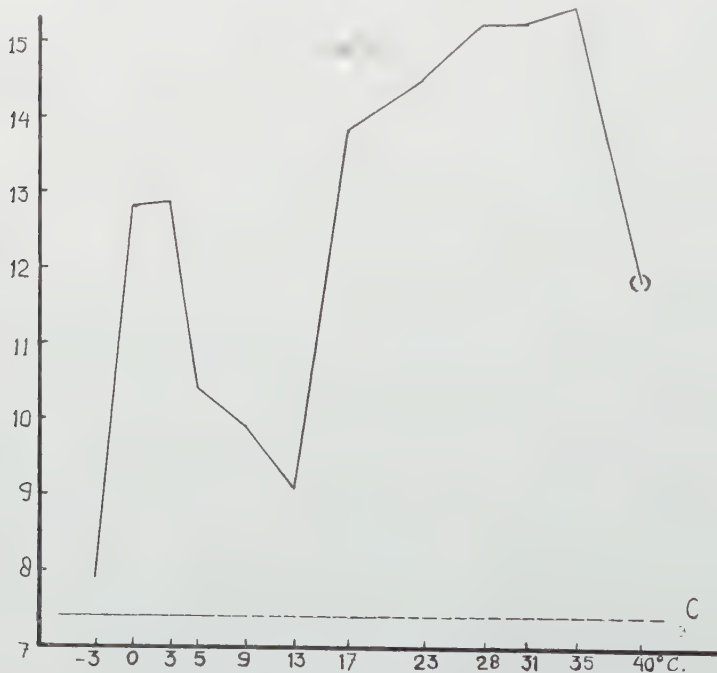


Fig. 8. Starch hydrolysis in extensive temperature range. Leaf discs from *H. annuus*. Exposition time 14½ h., 6 leaves. See further: caption of fig. 5. Exp. of 29-30 September 1950.

Fig. 9 represents the experiment, already alluded to, in which starch hydrolysis in relation to temperature was investigated in leaves connected with a large stem piece. The set-up was as follows. Three stems (each including the stem tip) were placed in a large bottle with water, in each temperature. The three stems belonged to three different plants, A, B, C, but all A's (in the various temperatures) were of the same plant. So were all B's and all C's. The temperatures

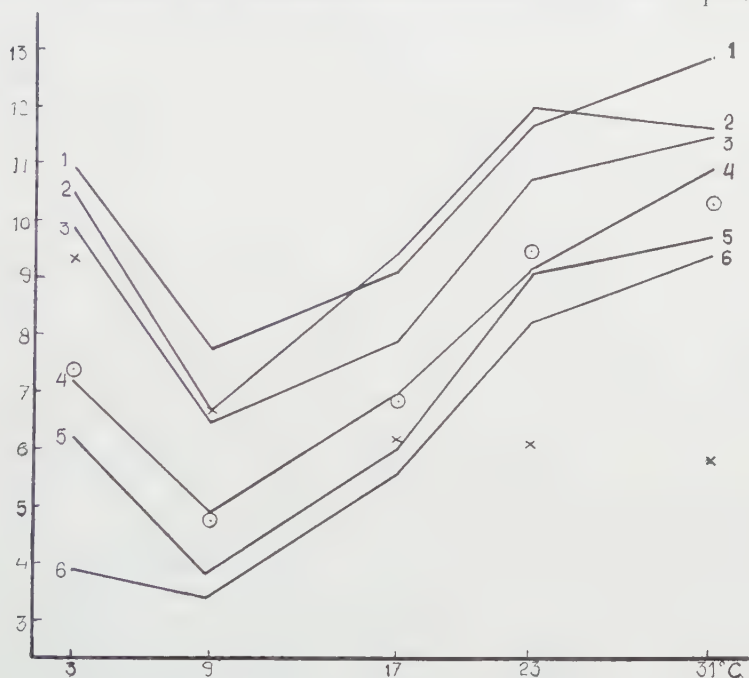


Fig. 9. Starch hydrolysis in relation to temperature. Discs from leaves of *H. tuberosus* attached to large stem pieces. 1-6 increasing age of leaves. Each point average of 3 sprouts. Ordinates: Difference in light transmission values at the end of the experiment as compared with the controls at the start. Curves 1-6 average of 3 (in some cases 2) values. See Table 3. For the sake of clarity, the ordinate of curve 1 has been increased by 2 units, that of curves 2 and 3 by 1 unit. ○ average of curves 1-6, × distance between curves 1 and 6 (as plotted) in order to illustrate the special difference at 3° C. Exp. of 4-5 October 1950.

chosen were 3°, 9°, 17°, 23° and 31° C. A disc was cut out of each of 6 leaves from each stem at the start of the experiment, as follows. About three uppermost visible leaves were left untouched, these being too small. The next leaf was the leaf No. 1 (fig. 9); leaf No. 2 was 2 leaves down from 1, No. 3 was 2 leaves down from 2, etc. Under No. 6, the stem pieces still had 4 leaves, and below that, a defoliated stem piece of about 12 cm was left. A corresponding disc from every leaf used was cut out at the end of the experiment. The experimental period was about 15 hours.

Each point of the curves, obviously, is the average of 3 values

TABLE 3

Data on starch hydrolysis in *Helianthus tuberosus* (expressed as light transmission values) in relation to temperature in leaves of various ages, attached to large stem pieces. The data "Experiment minus control" are plotted in fig. 9. C = control. Exp. of 4-5 October 1950.

Plant	Leaf	3		9		17		23		31°	
		C	Exp.	C	Exp.	C	Exp.	C	Exp.	C	Exp.
A	1	5.4	13.4	5.5	8.7	2.2	4.2	5.0	13.6	2.5	12.0
B	1	4.5	15.0	2.3	9.5	4.0	14.0	2.7	13.3	1.8	14.0
C	1	4.0	12.0	4.2	11.0	5.6	14.7	3.3	13.3	1.3	12.8
Sum		13.9	40.4	12.0	29.2	11.8	32.9	11.0	40.2	5.6	38.8
Average		4.6	13.5	4.0	9.7	3.9	11.0	3.7	13.4	1.9	12.9
Exp. minus control		8.9		5.7		7.1		9.7		11.0	
A	2	5.3	14.3	5.5	10.0	3.0	9.0	6.0	14.8	5.2	14.0
B	2	4.5	15.0	3.2	10.0	4.0	13.2	2.5	15.6	1.8	13.0
C	2	4.0	13.0	—	—	4.0	14.3	4.0	16.0	1.7	13.8
Sum		13.8	42.3	8.7	20.0	11.0	36.5	12.5	46.4	8.7	40.8
Average		4.6	14.1	4.4	10.0	3.7	12.2	4.2	15.3	2.9	13.6
Exp. minus control		9.5		5.6		8.5		11.1		10.7	
A	3	5.1	12.4	7.2	10.5	5.0	9.1	4.2	12.4	4.8	12.3
B	3	4.0	14.5	—	—	5.3	15.0	—	—	3.0	14.5
C	3	—	—	7.0	14.6	—	—	6.3	17.8	1.6	14.3
Sum		9.1	26.9	14.2	25.1	10.3	24.1	10.5	30.2	9.4	41.1
Average		4.6	13.5	7.1	12.6	5.2	12.1	5.3	15.1	3.1	13.7
Exp. minus control		8.9		5.5		6.9		9.8		10.6	
A	4	7.0	11.8	5.0	8.0	4.7	8.0	4.7	13.3	2.2	10.3
B	4	3.2	12.0	5.0	10.3	5.3	12.7	2.4	12.3	3.0	15.6
C	4	4.0	12.0	3.2	10.7	3.0	13.2	—	—	1.4	13.7
Sum		14.2	35.8	13.2	28.0	13.0	33.9	7.1	25.6	6.6	39.6
Average		4.7	11.9	4.4	9.3	4.3	11.3	3.6	12.8	2.2	13.2
Exp. minus control		7.2		4.9		7.0		9.2		11.0	
A	5	4.8	10.0	2.0	6.2	3.0	5.0	4.3	12.4	2.4	9.6
B	5	4.3	12.0	7.0	9.8	6.5	14.3	2.8	12.5	4.6	15.8
C	5	2.2	8.0	9.0	13.4	3.0	12.0	3.3	13.0	2.0	13.1
Sum		11.3	30.0	18.0	29.4	12.5	31.3	10.4	37.9	9.0	38.5
Average		3.8	10.0	6.0	9.8	4.2	10.4	3.5	12.6	3.0	12.8
Exp. minus control		6.2		3.8		6.2		9.1		9.8	
A	6	8.0	9.8	4.0	7.3	2.5	6.0	6.0	12.8	3.8	10.3
B	6	4.5	9.2	7.7	7.6	6.0	12.0	6.2	15.0	3.0	13.4
C	6	3.7	8.8	7.6	14.4	3.3	10.5	2.3	11.4	2.0	13.4
Sum		16.2	27.8	19.3	29.3	11.8	28.5	14.5	39.2	8.8	37.1
Average		5.4	9.3	6.4	9.8	3.9	9.5	4.8	13.1	2.9	12.4
Exp. minus control		3.9		3.4		5.6		8.3		9.5	
Average of "Exp. minus control" leaves 1-6 . .		7.4		4.8		6.9		9.5		10.4	

(obtained from the corresponding leaf number of the 3 stems, A, B, and C). The corresponding blank also is the average of 3 values, obtained in a similar way. The difference of these averages is plotted in fig. 9 (see also Table 3).

The following conclusions can be drawn: 1. The curves do not differ conspicuously from those obtained with cut leaves or leaf discs. 2. Again, relatively high values at 3° and at 17° and higher are separated by a clear minimum at 9° C. 3. Leaves of all ages investigated behave in a virtually similar way. 4. There is a slight indication that the older leaves show a less conspicuous maximum of hydrolysis at low temperatures.

In some other experiments (figs 10, 11) leaves were brought successively under various temperatures. These experiments were set

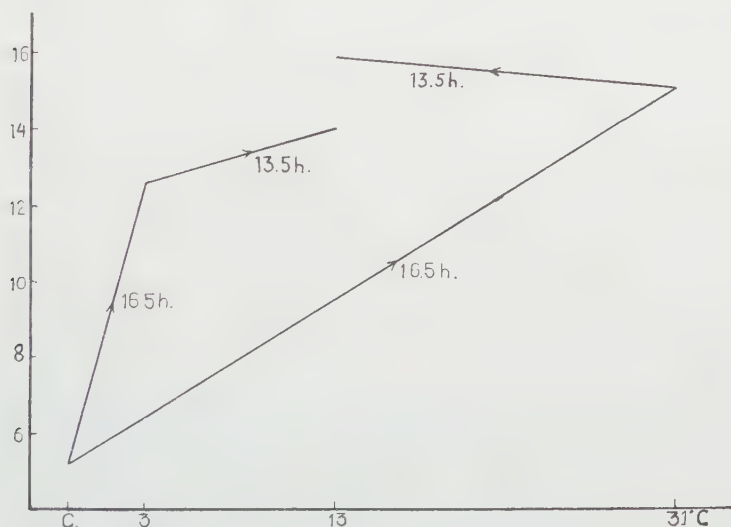


Fig. 10. Starch hydrolysis at 13° C in leaf discs of *Helianthus tuberosus*, after pre-exposure to 3° C and 31° C respectively. Ordinate at C = light transmission at the start. Duration of pre-exposures 16.5 h., of exposure to 13° C: 13.5 h. Ordinate: light transmission. Each point average of 6 leaf discs. Exp. of 9-10 October 1950.

up in order to attempt an elucidation of the minimum in the hydrolysis temperature curve. It must be mentioned first that, so far, no rates of partial processes have been measured along with the experiments. It would seem that the observed temperature curve might be explained by assuming three different processes, *viz.*, 1. hydrolysis of starch, 2. synthesis (or resynthesis) of starch, 3. respiration of sugars. It seems feasible to assume that these processes all have a positive temperature increment, but of different values, somewhat like schematically represented in fig. 12. According to this scheme, hydrolysis would develop the largest potential velocity of the three at low temperatures, and, since it does not rely upon the velocities of the two other ones, hydrolysis will actually predominate. In this temperature region,

sugars will accumulate. At average temperature, however, (re)-synthesis will acquire a rate commensurable to that of hydrolysis, thus counterbalancing hydrolysis to a large extent, and decreasing its observed gross rate. At still higher temperatures the potential rate of respiration will be the highest of the three, thus preventing re-synthesis by the removal of sugars produced by starch hydrolysis.

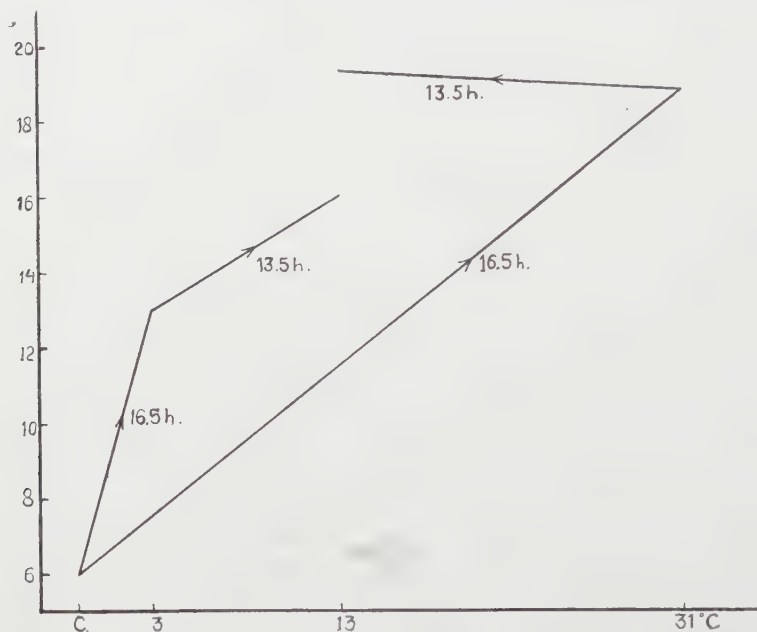


Fig. 11. The same as fig. 10, with *H. annuus*. Exp. of 9-10 October 1950.

(Actually, since respiration may be assumed to be limited by the amount of hydrolytic material formed, the curve of starch disappearance will again follow the hydrolysis curve). Two different situations have been represented in fig. 12, differing in the position of the synthesis curve. The position I would seem to imply that at medium temperatures hydrolysis would be completely prevented by the synthetic tendency, in the case II it would only be reduced in its gross rate. The experiments presented so far are in favour of case II (see below).

The experiments of figs 10 and 11 were made to investigate this point more directly. The idea was that, probably, a prolonged exposure to low temperature might increase the sugar content so much that, after transfer to about 13°, resynthesis of starch might be demonstrated. Under these conditions, pre-exposure at high temperature, would not be expected to lead to synthesis, since the sugars should be removed by respiration.

The experiments were made in such a way that discs from the same leaf were brought in part to 3° C in part to 31° C, and left there for

16.5 h. After that, some were examined for starch hydrolysis having taken place, others were transferred to 13°C , and left there for another 13.5 h. Figs 10 and 11 show that both in *Helianthus annuus* and in *H. tuberosus* hydrolysis increases during the period at 13°C . It even may be remarked that hydrolysis at 13°C proceeds more strongly after pre-exposure to 3° than it does after pre-exposure to 31°C , especially in the case of *H. annuus*. It should not be overlooked, however, that the pre-exposure at 31°C had removed more starch already

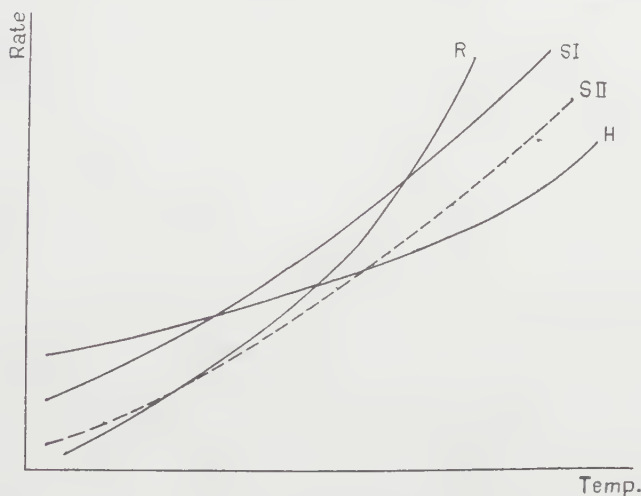


Fig. 12. Scheme representing possible increments of starch hydrolysis (H), (re-)synthesis of starch (SI and SII respectively) and respiration (R) in *Helianthus* leaves, in order to explain the minimum in the temperature-hydrolysis curve. See text.

then the pre-exposure at 3°C , so that no big further increase of the light transmission was to be expected. But the fact remains, that after preexposure to 3°C , no resynthesis of starch at 13°C can be demonstrated. The explanation may be that the situation corresponds to that of case II in fig. 12. On the other hand, resynthesis may obtain only at high local sugar concentrations, concurrent with hydrolysis in the neighbourhood of starch particles at suitable temperatures, and does not take place when the concentration of the sugar is decreased by diffusion.

c. Starch hydrolysis in relation to some other factors

A number of experiments has been made in order to investigate the influence of light on starch hydrolysis, the influence of the gas-phase, especially the oxygen content, and of the CO_2 content in relation to light. Also the admission of glucose and saccharose in various ways has been studied. Not all results obtained along these lines are as satisfactory yet as those obtained in the temperature studies, since certain experimental difficulties have not yet been fully eliminated. The following results seem to be worth mentioning.

Figs 13 and 14 show an experiment in which the influence of light of various intensities, including darkness has been studied at different temperatures. Daylight fluorescent tubes have been used for illumination. Six discs were put in petri dishes above 0.5 % KOH solution, the No. 1 disc in each petri dish coming from the same leaf, each No. 2 disc from a second leaf, and so on. The leaf material exposed in the various conditions (16 experiments and one control) thus is strictly comparable. No definite effect, consistent at all temperatures, could be traced. The only conclusion seems that under the conditions chosen (low carbon dioxide) no definite effect of illumination on

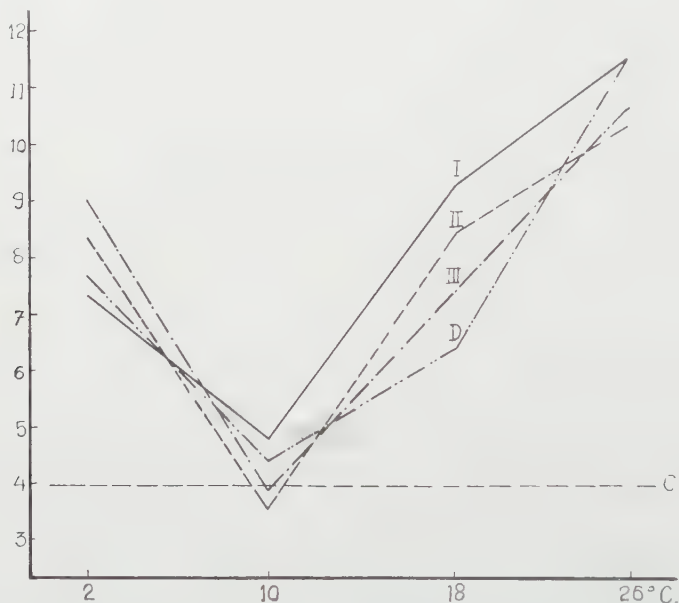


Fig. 13. Starch hydrolysis in relation to temperature at various light intensities. Leaf discs of *H. tuberosus*. Low CO_2 -concentration. Light intensities at 2° C: I \sim 2600 lux, II \sim 1300 lux, III \sim 650 lux; at 10° C: I \sim 2600 lux, II \sim 2100 lux, III \sim 1200 lux; at 18° C: I \sim 3400 lux, II \sim 1900 lux, III \sim 900 lux; at 26° C: I \sim 5000 lux, II \sim 2100 lux, III \sim 900 lux; D = dark. See further caption of fig. 5. Exp. of 11–12 October 1950.

starch hydrolysis has been found, neither in *H. tuberosus*, nor in *H. annuus*. All curves show the characteristic temperature dependence, as described earlier in this paper, with a minimum at 10° C. This minimum is more pronounced in *H. tuberosus* than in *H. annuus*, which is also in accordance with what was mentioned above.

In 1951, some series of experiments with *H. tuberosus* were made in order to investigate the influence of CO_2 , in the presence and absence of light. Leaf discs were exposed in glass jars (so called dissiccators were used) which were filled either with normal air or with air enriched with 5 % CO_2 . The results are given in Table 4. Light + CO_2 definitely decreases hydrolysis as compared with darkness + CO_2 or

with light — air. This seems to indicate, that photosynthesis counteracts starch hydrolysis in the presence of CO₂. This time, in air, also a difference between light and darkness is observed. But also in darkness, hydrolysis is definitely less in the presence of 5 % CO₂, which

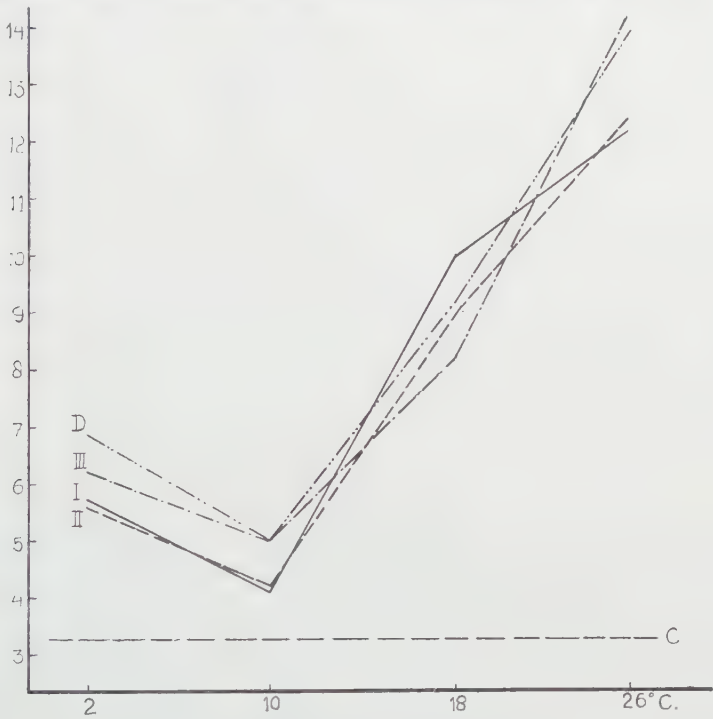


Fig. 14. The same experiment as fig. 13, with *H. annuus*. Exp. of 11–12 October 1950.

TABLE 4
Influence of light and darkness on starch hydrolysis in leaf discs of *Helianthus tuberosus* with and without CO₂ added.

Date	Air + 5 % CO ₂ , light	Air + 5 % CO ₂ , darkness	Air, light	Air, darkness	Control
1951					
30/8–31/8	2.7	2.8	4.6	5.5	1.2
31/8– 1/9	2.3	2.0	2.4	3.3	0.6
5/9– 6/9	3.8	8.3	7.1	9.4	1.6
12/9–13/9	2.0 *	8.2 *	5.3	9.6	1.0
13/9–14/9	1.6	3.8	3.0	6.6	1.0
14/9–15/9	1.2	5.6	4.9	7.1	1.3
Average	2.3	5.1	4.6	6.9	1.1
Average II	(2.3	4.5	4.4	6.4	1.1)

* These values were found in the reverse order as indicated here. It seems certain that both vessels with the leaf discs in iodine solution have been interchanged. Omitting this experiment, the average values of the remaining 5 experiments are as indicated in the last horizontal line (Average II).

seems to point to some harmful effect of the CO_2 -tension used. The experiments were made at about 25°C .

Already in 1950, it has been tried to study the effect of sugars on starch hydrolysis, by observing leaf discs in glucose or sucrose solutions of low depth, or a shaking machine. The results had not been very satisfactory. In some new attempts leaf discs were infiltrated with sugar solutions in vacuo, dried superficially afterwards, and then submitted to conditions for starch hydrolysis. In all cases the infiltration with various strengths of sugar solution counteracted hydrolysis, but so did also infiltration with water. This result was interpreted to mean that removal of air from the intercellular spaces probably interfered with various aspects of the metabolism of the leaf.

This lead to experiments in which hydrolysis of starch in leaf discs was investigated in a gasphase of nitrogen containing different amounts of oxygen. In most of the experiments, 6 leaf discs were placed in tubes of about 100 ml. contents, with a rubber stopper having in- and outlet for gas. All experiments were made in darkness at 5° and 25°C . Some of the results are collected in Tables 5 and 6. It was observed that leaf discs, exposed in nitrogen, showed black spots at the end of the experiment. It was thought that a more or less quantitative idea of the damage done could be obtained by

TABLE 5

Transmission of leaf discs of *Helianthus tuberosus* before iodine staining, in connection with the oxygen content of the gas phase (see text). Exps. of various dates.

Date	25°C		Control	5°C		Remarks
	Air	N_2		Air	N_2	
1951						
17/9-18/9	34.5	32.7	31.6	35.0	22.3	Pure nitrogen
18/9-19/9	35.8	6.1	32.3	36.6	33.1	" "
19/9-20/9	38.0	24.6	34.4	37.4	35.8	" "
20/9-21/9	35.9	7.7	30.0	35.2	34.2	" "
21/9-22/9	35.1	7.8	33.4	34.4	31.4	" "
Average	35.9	15.8	32.5	35.7	31.4	
25/9-26/9	33.5	31.5	25.7	35.1	32.4	N_2 , containing 3.83 % O_2
26/9-27/9	29.7	16.4	28.7	28.7	27.3	" " " "
27/9-28/9	28.4	17.9	21.0	26.5	21.7	" " " "
Average	30.5	21.9	25.1	30.1	27.1	
1/10-2/10	32.8	28.6	27.5	31.7	31.3	N_2 , containing 5 % O_2
2/10-3/10	33.5	24.3	29.7	33.0	31.2	" " " "
3/10-4/10	32.1	29.3	29.6	32.1	31.9	" " " "
4/10-5/10	32.1	28.8	29.3	32.4	30.1	" " " "
Average	32.6	27.8	29.0	32.3	31.1	
5/10-6/10	30.6	26.1	26.4	29.8	28.1	N_2 , containing 10 % O_2
8/10-9/10	30.0	29.2	26.8	28.7	28.8	" " " "
Average	30.3	27.7	26.6	29.3	28.5	

measuring the light transmission of the discs before colouring with iodine solution. These data are collected in Table 5. It is seen that, in pure nitrogen, mostly the light transmission is strongly decreased at 25° C, owing to the dark spots. These dark spots obviously arise through the action of oxidases, set free by the disorganization of certain cell complexes. Also at an oxygen tension of 3.83 %, this influence still is evident, and some slight remainders of it are seen at 5 and 10 % O₂. At 5° C, this effect is only very slightly, if at all perceptible. Only in pure nitrogen the average transmission value of the leaf discs is slightly lower than that of the controls. In air, the transmission values show no differences at 5° and 25° C. They are even higher than those of the controls. This last mentioned fact is

TABLE 6

Transmission of iodine-stained leaf discs of *Helianthus tuberosus* (see text) in connection with the oxygen content of the gas phase. Exps. of various dates.

Date	25° C		Control	5° C		Remarks
	Air	N ₂		Air	N ₂	
1951						
17/9-18/9	10.5	4.7	2.4	13.1	4.0	Pure nitrogen
18/9-19/9	10.9	2.6	3.2	12.9	9.3	" "
19/9-20/9	14.6	11.0	2.5	13.4	5.2	" "
20/9-21/9	10.3	2.1	1.7	12.1	3.9	" "
21/9-22/9	7.4	1.8	2.0	11.0	3.3	" "
Average	10.7	4.4	2.4	12.5	5.1	
25/9-26/9	8.5	7.3	1.4	13.0	5.2	N ₂ , containing 3.83 % O ₂
26/9-27/9	7.9	8.7	2.0	11.9	7.0	" " " "
27/9-28/9	10.1	6.4	1.6	11.5	5.1	" " " "
Average	8.8	7.5	1.7	12.1	5.5	
1/10-2/10	10.1	7.7	1.6	9.7	4.9	N ₂ , containing 5 % O ₂
2/10-3/10	12.8	8.9	2.0	11.4	7.4	" " " "
3/10-4/10	5.4	4.0	1.3	9.5	4.0	" " " "
4/10-5/10	10.2	9.2	1.9	13.5	8.0	" " " "
Average	9.6	7.5	1.7	11.0	6.1	
5/10-6/10	6.5	3.0	1.5	9.0	5.0	N ₂ , containing 10 % O ₂
8/10-9/10	6.4	4.3	1.9	9.0	4.3	" " " "
Average	6.5	3.7	1.7	9.0	4.7	

not well understood; the explanation might be that the larger amount of starch, present in the control, decreases the light transmission value by back scattering of light. At 5°, in nitrogen with 5 or 10 % O₂ the transmission values are not sensibly different from those in air, thus, no damage is perceivable in this way.

Looking at Table 6, in which the light transmission of the iodine stained leaf discs are given, we see that in all cases, starch hydrolysis in nitrogen is much less than in air, also at 5° C and even with 10 %

oxygen. It is remarkable that, invariably, hydrolysis in air was found more extensive at 5° than at 25° C. This seems slightly different from the experience obtained in the temperature series. It may be connected with the small air space available for the leaf discs, and it may be due to a relative lack of oxygen, or to some harmful excretion of the leaf discs into the atmosphere. The difference between air and the various low oxygen tension gas phases shows, that both at 5° and 25° C, oxygen promotes starch hydrolysis. Whether this influence is a direct one on the process of starch hydrolysis *sensu stricto*, or an indirect one via the metabolism of the leaf disc as a whole, cannot be inferred from the present experiments. The latter possibility seems the more likely one.

TABLE 7

Transmission of leaf discs of *Helianthus tuberosus* in connection with the oxygen content of the gas phase (see text). Experiments in dissiccators. Exps. of various dates.

Date	25° C		Control	5° C	
	Air	N ₂		Air	N ₂
A. Prior to iodine staining					
1951					
15/10-16/10	30.8	27.2	27.7	28.3	26.6
16/10-17/10	26.5	27.8	18.1	27.9	28.6
17/10-18/10	28.4	24.6	27.1	29.0	29.1
18/10-19/10	29.3	25.3	25.1	25.9	27.4
19/10-20/10	27.1	22.3	24.1	27.4	26.1
23/10-24/10	30.5	24.5	27.4	31.1	27.1
24/10-25/10	30.3	28.1	24.6	29.7	27.9
25/10-26/10	30.4	24.3	26.9	28.5	28.8
Average	29.2	25.5	25.1	28.5	27.7
B. After iodine staining					
15/10-16/10	20.7	15.0	7.2	19.4	17.0
16/10-17/10	16.3	14.2	—	19.7	18.4
17/10-18/10	—	20.8	11.6	21.7	21.6
18/10-19/10	20.3	—	8.2	19.9	17.2
19/10-20/10	19.1	17.3	6.3	18.6	—
23/10-24/10	—	21.0	12.2	21.5	16.4
24/10-25/10	24.1	21.8	9.1	21.3	—
25/10-26/10	28.1	22.3	—	23.7	22.0
Average	21.4	18.9	9.1	20.7	18.8
C. Averaging only those experiments from Part B in which corresponding alternatives in air and N ₂ are available.					
	20.7	15.0		19.4	17.0
	16.3	14.2		19.7	18.4
	19.1	17.3		21.7	21.6
	24.1	21.8		19.9	17.2
	28.1	22.3		21.5	16.4
				23.7	22.0
Average	21.7	18.1		21.0	18.8

At the end of the season, experiments on the effect of an atmosphere of nitrogen on starch hydrolysis in leaf discs at 5° and 25° C have been made, using dissiccators in order to avoid the eventual harmful influence of the small gas space. These series have not been worked out immediately, and some of the series were lost because the ethanol in which they were stored, had dried up. A drawback, moreover, was, that the guarantee against leakage was considerably smaller in the case of the dissiccators. Table 7 summarizes the available data. A higher illumination standard was used for the starch determinations so that the absolute transmission values are not directly comparable to those of the earlier series. Each figure in the Table is the average of 6 leaf discs. Considerable starch hydrolysis has taken place in all cases. The difference between air and nitrogen is considerably less than in the experiments in which tubes were used. Notwithstanding the fact that the dissiccators were ventilated with pure nitrogen (from bomb, not passing a reduction oven) and in some cases evacuated before, the results are nearer to those obtained in tubes when the gas contains some percents of oxygen. Small leakages of the dissiccators cannot be fully excluded as contributors to this result. The experiments of the effect of oxygen will have to be continued.

4. SUMMARY

Starch hydrolysis in leaves of *Helianthus tuberosus*, a short day variety, and in leaves of *H. annuus*, flowering in long day, was investigated by a simple colorimetric starch estimation *in situ* (§ 2).

Leaf halves, leaf discs, and leaves attached to considerable stem pieces, did not show conspicuous differences in starch hydrolysis. Moreover, the daily course of starch synthesis and breakdown was studied under natural conditions (figs 2, 3).

The temperature curve of starch hydrolysis mostly shows a pronounced maximum at about 0-3° C, a minimum around 10° C, and a renewed increase at temperatures above 15° C (figs 4-9).

An attempt has been made to explain the observed behaviour by assuming three processes, all possessing a temperature curve with a normal, positive rate increment with respect to temperature, *viz.*, starch hydrolysis, (re)synthesis of starch, and respiration of sugars (fig. 12).

Experiments on the effect of certain temperature sequences (3°, 13°; 31°, 13°) made in connection with the above tentative explanation of the temperature curve, failed to demonstrate a difference in behaviour at 13° C, depending on the preceding temperature. No re-synthesis of starch at 13° C after hydrolysis at 3° C was found. The reason may be that during a preceding period of hydrolysis at a temperature which is not suitable for (re)synthesis, the sugar concentration is lowered too much by diffusion, thus preventing effective resynthesis (figs 10, 11).

The temperature curve, in *H. tuberosus*, was found to be much the same in leaves of various physiological ages (fig. 9).

In air with low CO_2 content, light of various intensities was found not to influence starch hydrolysis in *H. tuberosus*, at various temperatures (figs 13, 14). In other experiments, 5 % CO_2 in air decreased hydrolysis considerably in light, but also in darkness (at 25°C) (Table 4), and this time, also in air a difference between light and darkness was found.

Lack of oxygen was found to decrease starch hydrolysis, especially at high temperature. (Table 5, 6). In large gas spaces this effect was less than in small ones, but in the large gas spaces used (dissiccators) anaerobiosis may not have been fully satisfactory (Table 7). The study of the influence of the composition of the gas phase still is incomplete.

Attempts were made to study the effect of sugar solutions on starch hydrolysis. In many cases a decrease in hydrolysis was found, but it was observed that also water could bring about similar effects, bringing the phenomenon into contact with the effects of lack of oxygen. These experiments, therefore, still were felt to be unsatisfactory.

It was observed occasionally that wilting promotes starch hydrolysis.

REFERENCES

1. HASSID, W. Z. and E. W. PUTMAN, *Ann. Rev. Plant Physiol.* 1: 109-124. 1950.
2. SACHS, J., *Arb. Bot. Inst. Würzburg* 3: 1-33. 1884, also in *Gesamm. Abhandl. Pflanzenphysiol.* 1: 354-387. Leipzig, 1892. Cf. p. 357.
3. WASSINK, E. C. and C. VAN DER SCHEER, *Meded. Landbouwhogeschool Wageningen, Netherlands* 51: 175-183. 1951.

NOTES ON THE ARACEAE OF SURINAME

BY

A. M. E. JONKER-VERHOEF AND F. P. JONKER

Botanical Museum and Herbarium, Utrecht

(Received April 14th, 1953)

The list of *Araceae* published in 1906 by A. A. PULLE in his "Enumeration of the Vascular Plants known from Surinam" comprises 39 species belonging to 14 genera, the largest genera being *Anthurium* with 7 species and *Philodendron* with 12 species. It was found that one of these 39 species was included by mistake, for the specimen Wullschlaegel n. 1764, which is the type of *Spathiphyllum blandum* Schott, was erroneously assumed to have been collected in Suriname.

Already in 1908 TRESLING had collected a species that was not listed by PULLE, viz. *Dieffenbachia picta* (Lodd.) Schott.

Our studies of the collections made between 1915 and 1926 by the Forestry Department (B.W.) revealed the presence of 5 hitherto unrecorded species, viz. *Anthurium digitatum* (Jacq.) G. Don, *Dieffenbachia paludicola* N. E. Br. ex Gleas., *Heteropsis jenmanii* Oliv., *Philodendron guttiferum* Kunth and *Spathiphyllum huberi* Engl.

In 1937 during the expedition to the southern frontier of Suriname the physician ROMBOUTS collected another species that proved to be new to the flora, viz. *Anthurium clavigerum* Poepp.; it was previously known from Peru only.

The entomologist GEYSKES increased in 1939 the total number of species by two by collecting *Heteropsis longispathacea* Engl., so far known from Amazonian Brazil only, and the noteworthy *Anthurium salviniae* Hemsley, previously known from Guatemala and Yucatan.

In 1944 STAHEL recorded for the first time the occurrence in Suriname of the genus *Heteropsis*, of which the most common species, *H. jenmanii* Oliv., originally described from British Guiana, had already been collected several times by the Forestry Department.

In 1948 A. D. HAWKES published in the Bulletin of the Torrey Botanical Club 75, p. 633, an enumeration of the *Araceae* collected in 1944 by Bassett MAGUIRE. His list contains the names of 10 species that were recorded here for the first time as collected in Suriname, and 4 of these were regarded as entirely new. The number of genera was increased by two, viz. *Stenospermation* Schott and the new genus *Maguirea*. The number of species that were said to be new to the Suriname flora and also the number of new species appeared to be remarkably large when the figures for the *Araceae* are compared with those for other families represented in MAGUIRE's collection. Though our revision showed that some of HAWKES' identifications were incorrect, the MAGUIRE collections nevertheless proved to contain some

important additions to the list of Suriname *Araceae*, viz. five hitherto unrecorded species, 3 of which were new, viz. *Anthurium maguirei* A. D. Hawkes, *Stenospermation maguirei* Jonk. et Jonk. and *Schismatoglottis americana* Jonk. et Jonk., and two new genera, viz. *Stenospermation* Schott and *Schismatoglottis* Zoll. et Mor. *Maguirea* A. D. Hawkes, however, proved to be identical with *Dieffenbachia* Schott (v. infra).

Finally the collections made by LANJOUW and LINDEMAN in 1948 proved to contain 2 species that were new for Suriname, viz. *Philodendron jenmanii* Krause, previously known from British Guiana and Amazonian Brazil, and *Syngonium hastifolium* Engl., known from Amazonian Brazil only.

As a result of our revision 18 genera, 56 species and 7 varieties of *Araceae* are now known from Suriname; 4 of these species are found as cultivated plants only. Of the 18 genera two are represented by a considerable number of species, viz. *Anthurium* Schott by 11 species and *Philodendron* Schott by 13 species; two of these *Philodendron* species proved to be represented by 2 varieties. The genus *Xanthosoma* Schott comes next with 5 species, of which 3 are known in Suriname as cultivated plants only. It is followed by the genus *Monstera* Adans. with 4 species. Both *Spathiphyllum* Schott and *Dieffenbachia* Schott have 3 species, but one of the species of *Dieffenbachia* is represented by 3 varieties.

Represented by 2 species are the genera *Dracontium* L., *Heteropsis* Kunth, *Montrichardia* Crueger, *Stenospermation* Schott and *Syngonium* Schott; whereas the genera *Caladium* Vent., *Cyrtosperma* Griff., *Rhodospatha* Poepp., *Pistia* L., *Schismatoglottis* Zoll. et Mor. and *Urospatha* Schott are represented by a single species; the only species of the last named genus is represented by 2 varieties. The genus *Colocasia* Schott is also represented by a single species but the latter is cultivated only.

It is noteworthy that some of the above mentioned genera have their main area in other parts of the world, viz. *Cyrtosperma*, of which 9 species occur in tropical Africa, Malesia, Melanesia and Polynesia and but 2 species in Amazonian Brazil and Guiana, and *Schismatoglottis*, with circ. 75 species in Malesia and Birma and a single species in Suriname. The genus *Spathiphyllum*, on the other hand, is represented by 26 species in tropical America and only 1 in Malesia. The genus *Pistia*, which consists of a single aquatic species, is pantropic, but all the remaining genera occurring in Suriname are confined to tropical America. Among them *Heteropsis* shows the smallest area of distribution, for it is restricted to Brazil and Guiana.

In the following paper a few taxonomic and phytogeographic remarks are made on some of the genera and species. There are also descriptions of two new species.

DRACONTIUM L.: *D. foecundum* Hook.f., known from Trinidad and British Guiana, is to be expected in Suriname as it was collected twice on the British bank of the Corantyne River. Known from Suriname are *D. asperum* K. Koch and *D. polyphyllum* L.

CYRTOSPERMA Griff.: this genus has but once been found in Suriname and this collection has to be referred to *C. spruceanum* (Schott) Engl., not to *C. americanum* Engl. as was done by PULLE. *C. americanum* is known from French Guiana only.

UROSPATHA Schott: PULLE mentioned *U. hostmannii* Schott only. Now more material of this genus has been collected, and this does not belong to *U. hostmannii* but, in our opinion, to *U. sagittifolia* (Rudge) Schott. We consider *U. caudata* (Poepp.) Schott as conspecific with the latter.

According to ENGLER the difference would be that *U. sagittifolia* has a rough and verrucose petiole and *U. caudata* a smooth one. This feature, however, is of no value as the petiole is often rough towards the base and smooth in the upper part. GLEASON too appears to have come to this conclusion for he remarked on a label attached to Jenman n. 5779 in the Kew herbarium: "The petiole is smooth at the apex but becomes rough towards the base so that *U. caudata* and *U. sagittifolia* are one species".

The other difference mentioned by ENGLER, viz. the length of the denudate part of the main ribs in the basal lobes of the leaf blade, has no value either as the variability of this character is so great that no line can be drawn. *U. hostmannii* is regarded by the present authors as a variety of *U. sagittifolia*, characterized by the narrower leaves and we consider *U. spruceana* Schott, *U. decipiens* Schott and *U. dubia* Schott identical with this variety. Its correct name appears to be *U. sagittifolia* (Rudge) Schott var. *spruceana* (Schott) Engl. Both SCHOTT and ENGLER mention as type of *U. spruceana* Schott the specimen "Spruce n. 945". However, 945 is not the collector's number but the number given to this collection in the MARTIUS herbarium. The correct collector's number is 1235; this number is cited both by SCHOTT and ENGLER as the type of *U. decipiens* Schott.

ANTHURIUM Schott: in the genus *Anthurium* PULLE cited 7 species but one of them, viz. *A. trinerve* Miq. we consider conspecific with *A. scandens* (Aubl.) Engl., which was also cited by PULLE. The two collections referred by PULLE to *A. acaule* Schott do not belong to this species but to *A. gracile* (Rudge) Engl., a species also cited by him. To the remaining 5 species, A. D. HAWKES, l.c., added in 1948: 1°. *A. galeottii* (Hort.) C. Koch; the specimen cited by him, however, belongs to *A. scolopendrinum* (Ham.) Kunth, which was mentioned already by PULLE; 2°. *A. hookeri* Kunth, the specimen is named by the present authors *A. crassinervium* (Jacq.) Schott, see below; 3°. a new species, *A. maguirei* A. D. Hawkes; 4°. *A. nigrescens* Engl.; this specimen is regarded by the present authors as belonging to *A. polyrrhizum* C. Koch et Augustin; 5°. another new species, *A. stahelii* A. D. Hawkes, which, however, does not belong to this genus but to *Philodendron* Schott, and is conspecific with *P. myrmecophilum* Engl. Three of these species therefore have to be added to the five good species of PULLE's list, which brings the number to eight. To these

eight we added as a result of the study of our unidentified material: *A. salviniae* Hemsl., *A. clavigerum* Poepp. and *A. digitatum* (Jacq.) G. Don. Consequently 11 species of *Anthurium* are now known from Suriname. It seems desirable to give a few taxonomic and phyto-geographic notes on some of the species of this genus.

Noteworthy is the discovery by GEYSKES of *A. salviniae* Hemsley in the Toemock-Hoemoek Mts. Up till now this species was known from Guatemala (Heyde and Lux n. 4278 [K] and Salvin s.n. [K]) and Yucatan (A. Schott n. 638 [BM]).

The correct names of the large-leaved rosulate not rarely cultivated *Anthurium* species which are known as *A. crassinervium* (Jacq.) Schott and *A. hookeri* Kunth, were not easy to determine. The type of *A. hookeri*, figured by HOOKER in Botan. Magaz. t. 2978 as *Pothos crassinervium* Jacq., has a rather short, cylindrical spadix. According to ENGLER, in Das Pflanzenr. IV. 23B (1905), p. 77, Fig. 24, *A. crassinervium* (Jacq.) Schott has a rather long, narrowly cylindrical spadix. The original plate of JACQUIN, Icon. III (1793), t. 609, however, shows a short, cylindrical spadix. The type material of JACQUIN in the Vienna herbarium was destroyed by war action. The herbarium of the British Museum, Natural History, at London possesses a specimen named *Pothos crassinervium* Jacq., Icon. hort. Vindob., which has a short cylindrical spadix.

If this specimen were accepted as isotype, HOOKER would have been correct in referring his specimen to *A. crassinervium* (Jacq.) Schott and *A. hookeri* Kunth would be synonymous with *A. crassinervium* (Jacq.) Schott.

In that case a new name would have to be found for the species with the long, narrowly cylindrical spadix, i.e. for the species to which the material collected in Suriname belongs. However, as it is not certain that the specimen in the British Museum is an isotype, the present authors named the material from Suriname *A. crassinervium* (Jacq.) Schott, basing their identification on the figure given by ENGLER, l.c., and conforming to the generally accepted view. They disagree therefore with A. D. HAWKES who identified the Suriname material collected by MAGUIRE as *A. hookeri* Kunth. ENGLER wrongly considered *A. huegelii* Schott conspecific with *A. hookeri* Kunth; the base of the leaf blade is in these two species quite different. The description of *A. hookeri* given by ENGLER, l.c., is consequently highly confused, see also N. E. BROWN in Gardn. Chron. 48 (1910), p. 153.

Anthurium martianum C. Koch et Kolb is said to have been collected in Suriname and brought into culture. Material from cultivation is preserved in the herbaria B and M, but none of the herbaria possess material of this species collected in Suriname.

Anthurium scandens (Aubl.) Engl. is cited by PULLE from Suriname. He also mentioned *A. trinerve* Miq., which differs, according to ENGLER, by peduncles that are twice to three times as long as the petioles, the peduncles and petioles of *A. scandens* being of equal length. *A. trinerve* Miq. however is a later homonym of *A. trinervium* Mart. In our opinion, however, there is no difference between the common

A. scandens, known from the West Indies and Guiana, and *A. trinerve* Miq., known from Guiana and Amazonas. Consequently we unite the two species under the name *A. scandens* (Aubl.) Engl. and consider *A. trinerve* Miq. = *A. brachyspathum* C. Koch et Bouché and also *A. scandens* var. *violaceum* (Sw.) Engl. synonyms. If this is agreed *A. scandens* (Aubl.) Engl. becomes the most common species in this genus.

A. digitatum (Jacq.) G. Don, once collected in Suriname (B.W. n. 4169), is very variable in the number of leaflets that compose the subdigitate leaf. According to ENGLER this number is 9–13. We found, however, that in the specimen cultivated in the Aroid House in the Royal Botanic Gardens at Kew the number varies from 5–13. The first leaves have a smaller number of leaflets than the subsequent ones; as a rule there are more than 5 leaflets. The same kind of variability, though in a smaller degree, was observed in *A. pentaphyllum* (Aubl.) G. Don; in this species the number of leaflets may vary from 3 to 9; as a rule we found 5. In both species the leaflets of the first leaves are sessile; in the subsequent ones the length of the petiolules in *A. pentaphyllum* may reach 2.5 cm, whereas in *A. digitatum* it may increase to 9 cm.

SPATHIPHYLLUM Schott: of this genus PULLE cited 3 species as known from Suriname, viz. 1°. *S. blandum* Schott, collected by WULLSCHLAEGEL (type), but this specimen was not collected in Suriname, the locality, "Bluefields, Mosquito, at the beach of the lagoon", being situated in the West-Indian Islands, probably in Jamaica; the species is not known from Suriname; 2°. *S. candolleianum* Schott; PULLE's specimen (Hostmann n. 1154) is regarded by the present authors as belonging to *S. humboldtii* Schott; and 3°. *S. cuspidatum* Schott; the specimen (Splitgerber s.n.) was cited by ENGLER and KRAUSE in Das Pflanzenr. IV. 23B (1908), p. 128, and was seen neither by PULLE nor by the present authors.

New to the flora of Suriname is *S. huberi* Engl., previously known from Brazil (Para) only. It was twice collected in Suriname.

STENOSPERMATION Schott: This genus was reduced by MACBRIDE in Field Mus. Nat. Hist. Bot. Ser. XL (1931), p. 6 to *Rhodospatha* Poepp. "since it has in general no distinction except the basal instead of lateral attachment of the ovules. If this character properly forms a basis of generic definition, other groups in the family now included under one name (as *Philodendron*, for example) should be segregated". We do not agree with this opinion. All *Philodendron* species have a 2- or more-celled ovary with axile placentation; the number of ovules, however, varies from several to few or even a single one in each cell; in the latter case this ovule is basal-axile. The genus *Rhodospatha*, however, has a 2-celled ovary with axile placentation, and the genus *Stenospermation*, on the contrary, has a one-celled or very incompletely 2-celled ovary, with a basal, annular placenta. The difference between *Rhodospatha* and *Stenospermation* is consequently greater and of more

fundamental importance than that between the *Philodendron* species. If *Rhodspatha* and *Stenospermatum* are united, then the genera *Heteropsis* and *Monstera* too would have to be included in the genus *Rhodspatha* s.l. There would even be more reason to unite the genera *Heteropsis* and *Monstera* for these two genera differ in general appearance only.

PULLE was not acquainted with the Suriname species of the genus *Stenospermatum*, but MAGUIRE collected two specimens, both named by HAWKES: *Stenospermatum spruceanum* Schott. A specimen collected in British Guiana was cited by him in the same paper as *Rhodspatha*



Stenospermatum maguirei

Jonk. & Jonk.

Fig. 1. a. flowering plant, b. leaf, c. spatha and spadix.

spruceana (Schott) Macbr. Consequently it is not possible to decide whether he agrees with the above mentioned opinion of MACBRIDE. The two specimens collected by MAGUIRE in Suriname, however, do not belong to *S. spruceanum* Schott. In our opinion one of them (Maguire n. 24459) belongs to *S. multiovulatum* (Engl.) N. E. Br., originally regarded by ENGLER as a variety of *S. spruceanum* Schott. The other one belongs to a new species, named by us in honour to its collector *Stenospermatum maguirei* Jonk. et Jonk. (fig. 1).

Stenospermatum maguirei n.sp. Caudex scandens, internodiis 1–1.5 cm longis. Foliorum petiolus 9.5–13.5 cm longus usque ad 1–3 cm infra laminam vaginatus, vagina apicem versus latitudine decrescente; lamina coriacea, elliptica, basi acuta, apice 1 cm longo acuminata, 15.5–22 cm longa, 3–4.5 cm lata. Pedunculus teres, robustus, circ. 2.5 cm longus. Spatha late-elliptica, decidua, circ. 6.5 cm longa, 3.5 cm lata, alba. Spadix stipite 8 mm longo suffultus, anguste cylindricus, 5 cm longus, 0.6 cm diam. Stamina 4.25 mm longa, 0.7 mm lata. Pistillum 1.7 mm longum, 2 mm crassum, ovario obconico, stylo discoideo, stigmatibus capitato. Ovula circ. 10, 0.5 mm longa, funiculi 0.5 mm longi. Typus: Maguire 24556 in herbario NY — Surinamo, in monte Tafelberg, altitudine 300 m.

This species differs from *S. multiovulatum* (Engl.) N. E. Br. by being a climber and by the leaf sheath which may nearly reach the base of the leaf blade and becomes gradually narrower towards the top. The leaf blade is acuminate and smaller than in *S. multiovulatum*. The inflorescence is erect. *S. spruceanum* Schott differs by its wider and more robust leaves and the obtuse to rounded apex of the leaf sheath.

RHODOSPATHA Poepp.: after the specimen cited already by PULLE as *R. oblongata* Poepp. (Wulfschlaegel n. 1570) no material of this genus was collected in Suriname. *Rhodospatha melinonii* (Engl.) Engl. et Krause, known only from French Guiana but collected as far westwards as the French bank of the Marowijne R., was included by the present authors in the genus *Heteropsis* Kunth (v. infra).

HETEROPSIS Kunth: according to PULLE, Enum. (1906), no material of this genus had been collected up till then. STAHEL, in 1944, for the first time mentioned the occurrence in Suriname of *H. jenmanii* Oliv. Under the vernacular name "kamina" this species was well known to the natives who used the aerial roots for making baskets and ropes. *H. longispathacea* Engl. was once collected in Suriname; its aerial roots are useless for making ropes. *Rhodospatha melinonii* (Engl.) Engl. et Krause is referred by the present authors to this genus. It is known from French Guiana only, but is to be expected in Suriname, as in French Guiana the species is rather common and has been collected i.a. on the French bank of the Marowijne River. Its transference to the genus *Heteropsis* is justified in our opinion by the fact that the cells of the 2-locular ovary each contain two basal ovules. This is found in the genera *Monstera* and *Heteropsis*, but by its general appearance the species fits much better in the latter and, moreover, the top of the

fruit is marginate which is typical for that genus. The name becomes therefore *Heteropsis melinonii* (Engl.) Jonk. et Jonk., nov. comb.

MONSTERA Adans.: the differences between this genus and the genus *Heteropsis* Kunth are mainly found in general appearance of the species.

In *Monstera* the petioles are longer, the leaf blades not so rigidly coriaceous as in *Heteropsis* and the fruits are not marginate at the apex. PULLE, l.c., mentioned 3 species from Suriname and later authors did not add other species. The most common one is *M. pertusa* (L.) De Vriese, regarded by ENGLER as "typus polymorphus". In our opinion the varieties of this species that were described by ENGLER, on account of differences in the leaves, are of little value, as the leaves vary greatly in the same plant. A collection of KEGEL, n. 236, incomplete material and consisting of a single leaf, was cited by PULLE, probably on the authority of a determination label signed by ENGLER, as *M. dilacerata* C. Koch. In our opinion this specimen very probably belongs to *M. pertusa*.

The remaining material was regarded by PULLE as belonging to *M. obliqua* Miq. In our opinion only the material with entire, narrow, falcate, oblique, elliptical leaves belongs to this species, and we consider *M. falcata* Engl., from Amazonian Brazil and Bolivia, and *M. fendleri* Krause, from Trinidad and Tobago, conspecific. The species was described by MIQUEL as a *Monstera* and not, as stated by ENGLER, as *Heteropsis obliqua*. The combination *Monstera obliqua* (Miq.) Engl. consequently is superfluous. The material with entire, wider, ovate leaves, included by PULLE in *M. obliqua*, belongs in our opinion to *M. sagottiana* Engl., earlier known from French Guiana.

PULLE also included in *M. obliqua* material with rather narrow, oblique, elliptical to ovate, fenestrate leaves. This belongs in our opinion to *M. expilata* Schott, which is considered by ENGLER a variety of *M. obliqua* (var. *expilata* (Schott) Engl.). *M. expilata* is known also from Amazonian Brazil and French Guiana.

Consequently in our opinion the number of *Monstera* species in Suriname is now four.

DIEFFENBACHIA Schott: PULLE knew from Suriname *D. seguina* (L.) Schott only. To this variable species, regarded by ENGLER as "typus polymorphus", still most specimens collected in Suriname are to be referred. The great variability, however, mainly originated in cultivation. In the material from Suriname it is possible to distinguish 3 varieties, of which the typical variety, according to Art. 35 of the International Code of Botanical Nomenclature var. *seguina*, was named by ENGLER var. *viridis* Engl.

According to ENGLER a specimen, collected in Suriname by WEIGELT and seen neither by PULLE nor by the present authors would belong to it. The remaining material belongs to the varieties *ventenatiana* (Schott) Engl. and *lingulata* (Mart. ex Schott) Engl.

Dieffenbachia picta Schott is perhaps but a variety of *D. seguina* with spotted leaves or even a mere form of *D. seguina* (L.) Schott var.

seguina. An incomplete specimen collected by TRESLING at the Upper Sipaliwini River, very probably belongs to it. On account of the variability of the cultivated material, it is considered by ENGLER a "typus polymorphus"; it is badly known. It has been recorded from Trinidad and Tobago and has perhaps also been found in Brazil.

D. paludicola N. E. Br. ex Gleas., a marsh plant known up till now from British Guiana only, was collected by the Forestry Department at the Corantyne River. MAGUIRE and STAHEL collected the species at Sectie O; this collection was described by A. D. HAWKES, l.c., as the type of a new species and a new genus: *Maguirea spathicarpoides* A. D. Hawkes.

SYNGONIUM Schott: the two species, cited by PULLE, viz. *S. affine* Schott and *S. vellozianum* Schott, are in our opinion conspecific. A difficulty was caused by the specific epithet. The oldest name quoted in the literature is *Xanthosoma? gracile* Miq., published in Delect. Sem. Hort. Amst. 1853. A type specimen has not been preserved, but in the Kew Herbarium we saw a drawing made by N. E. Brown of a specimen of *Xanthosoma gracile* Miq. preserved in the herbarium of C. KOCH. This drawing figures a plant with hastate leaves, which does not belong to one of the species mentioned above and the name *S. gracile* (Miq.) Schott consequently cannot be regarded as a synonym. *Arum auritum* Vell. is a later homonym of *A. auritum* L. and the correct name therefore is *Syngonium vellozianum* Schott. Of this species two varieties exist. The typical variety was named by ENGLER var. *latilobum* Engl. According to Art. 35 of the International Code of Botanical Nomenclature the varietal epithet must repeat the specific epithet without citation of the author's name; the correct name consequently is *S. vellozianum* Schott var. *vellozianum*. This variety has not been collected in Suriname. The Suriname material belongs to var. *poeppegii* Engl., later renamed by ENGLER var. *oblongisectum* Engl., but this name has to be rejected as illegitimate.

A second Suriname species was collected by LANJOUW and LINDEMAN in the Tibiti savannah, viz. *S. hastifolium* Engl.; it was previously known from Amazonian Brazil only.

XANTHOSOMA Schott: of the two species cited by PULLE, *X. conspurcatum* Schott has been collected only once, viz. by WULLSCHLAEGEL in 1851. *X. helleborifolium* (Jacq.) Schott var. *variegatum* (Desf.) Engl. is a seldom collected weed.

A number of *Xanthosoma* species are cultivated in tropical America as vegetables, for the edible rhizomes or as a fodder. STAHEL mentions for Suriname *X. sagittifolium* (L.) Schott; ENGLER mentions for Suriname *X. caracu* C. Koch et Bouché; and in the HERMANN herbarium from Suriname, preserved in the Botanical Museum and Herbarium at Utrecht, two leaves of *Xanthosoma belophyllum* (Willd.) Kunth are represented; they are said to be called Tayer leaves. Apart from this collection no specimens of these cultivated *Xanthosoma* species have been collected in Suriname.

CALADIUM Vent.: *C. bicolor* (Ait.) Vent. is spontaneous in Suriname, but is it also cultivated for the edible leaves and spadices. PULLE, partly following ENGLER, distinguished two forms. In our opinion the large number of varieties established by ENGLER and KRAUSE, are of little value. Most of these varieties have been based on material from cultivation. *C. schomburgkii* Schott is to be expected in Suriname, as it is known from French and British Guiana.

COLOCASIA Schott: *C. esculenta* (L.) Schott (= *C. antiquorum* Schott) is cultivated in nearly all tropical countries as a vegetable and also for the edible rhizomes. This is done in Suriname also, but it is impossible for us to decide to which varieties these plants may belong, as no specimens have been collected.

PHILODENDRON Schott: Pulle listed from Suriname 12 species. Of one of them, *P. splitgerberi* Schott, only leaves have been described. The type specimen was seen neither by PULLE nor by the present authors. Presumably it has been destroyed in the Vienna herbarium by war action.

Examination of the types of *P. linnaei* Kunth and of *P. decurrens* Krause revealed that they are conspecific and that the name of the latter therefore must be regarded as a synonym of the former. The type of *P. linnaei* (Dahlberg s.n.) has neither circ. 3 basal ovules in each ovary cell as stated by KUNTH nor 2 basal ovules as stated by SCHOTT and by ENGLER and KRAUSE, but each cell contains a small number of ovules spread over the whole length of the dissepiment.

Related is *P. insigne* Schott, which was collected three times in Suriname; it differs in the shape of the leaves and the size of the peduncles and leaf sheaths. In our opinion *P. calophyllum* Brogn. ex Linden et André must be regarded as a synonym of *P. insigne*. *P. laciniatum* (Vell.) Engl., cited by PULLE, was named by the present authors for reasons of priority *P. pedatum* (Hook.) Kunth. We stated the occurrence in Suriname of the var. *palmatisectum* (Engl.) Jonk. et Jonk., nov. comb. (= *P. laciniatum* (Vell.) Engl. var. *palmatisectum* Engl.). Contrary to what one would expect from the varietal epithet, the leaves of the variety are subpinnatisect.

Philodendron fragrantissimum (Hook.) Kunth has been collected in Suriname three times. *P. demerarae* Gleas. is a synonym. Maguire n. 23412, collected in British Guiana and cited by HAWKES as *P. demerarae*, however, does not belong to this species but to *P. pedatum* (Hook.) Kunth.

P. grandifolium (Jacq.) Schott and *P. acutatum* Schott (= *P. wulfschlaegeli* Schott = *P. cyclops* A. D. Hawkes) differ, according to our studies in: *a.* the shape of the leaf blade; *b.* the length of the peduncle: short in *P. grandifolium*, longer in *P. acutatum*; *c.* the ovary: in *P. grandifolium* 6-celled with 2 basal ovules in each cell and 9- or 10-celled in *P. acutatum* with several biseriate ovules in each cell.

The ovary of *P. grandifolium* is incorrectly figured in the drawing published by ENGLER and KRAUSE in Das Pflanzenr. IV. 23Db (1913), Fig. 21 as 5-celled with several ovules in each cell and incorrectly described by the same authors, i.e., as 10- to 12-celled with a small

number of ovules in each cell. According to the same authors the ovary of *P. acutatum* would be 6- to 8-celled.

P. grandifolium has twice been collected in Suriname, and *P. acutatum* ten times. *P. quinquenervium* Miq., cited by ENGLER and KRAUSE as a synonym of *P. acutatum*, is probably specifically distinct. If ENGLER and KRAUSE are right, however, the correct name for his species would be *P. quinquenervium* Miq. Kegel n. 946, cited by ENGLER and KRAUSE and by PULLE as *P. grandifolium*, belongs, according to our delimitation of the species (v. supra) to *P. acutatum* Schott.

From his study of the material collected by MAGUIRE, A. D. HAWKES added a number of species to those cited by PULLE. Among them is one new species: *P. cyclops* A. D. Hawkes. We reduce this species to *P. acutatum* Schott. New for Suriname would have been *P. nobile* Bull to which HAWKES referred Maguire n. 14405. In our opinion this specimen belongs to *P. insigne* Schott, which was already known from Suriname.

Our study of the unidentified material from Suriname produced a number of species new to this country, viz:

a. *P. myrmecophilum* Engl., previously known from Amazonian Brazil and now collected 4 times in Suriname. Maguire and Stahel n. 470, the type of *Anthurium stahelii* A. D. Hawkes belongs also to this species.

b. *P. jenmanii* Krause, previously known from British Guiana and Amazonian Brazil. It was collected in Suriname for the first time by LANJOUW and LINDEMAN in 1948. *P. scabrum* Krause is in our opinion a synonym.

c. *P. dioscoreoides* Gleas., previously known from British Guiana and, although known only in the sterile state, easily recognisable by its leaves.

d. *P. guttiferum* Kunth, previously already known from a great part of tropical America. *P. rudgeanum* Schott, cited by PULLE, was reduced by the present authors to a variety of this species, differing from the type in the short internodes of the branches (*P. guttiferum* Kunth var. *rudgeanum* (Schott) Jonk. et Jonk., nov. comb.). The variety is also known from Trinidad, British and French Guiana.

PULLE referred Kegel n. 850, on the authority of ENGLER, to *P. heterophyllum* Poepp. In our opinion it belongs to *P. sphalerum* Schott, already known from Suriname, where it was collected by SPLITGERBER. This specimen (Splitgerber s.n.), the type specimen, was seen neither by the present authors nor by PULLE or ENGLER. The transfer of the above-mentioned specimen to *P. sphalerum* means that *P. heterophyllum* Poepp. does not occur in Suriname.

The number of *Philodendron* species from Suriname has now been raised to 13; two of these species proved to be represented by 2 varieties. Not yet collected but to be expected are: 1. *P. eordatum* Schott, known from Brazil, French and British Guiana and according to a verbal information by N. Y. SANDWITH common and conspicuous in British Guiana though rarely flowering. In our opinion the variety *poiteauanum* (Schott) Engl. of this species is of no value.

2. *P. longepetiolatum* Engl., known from French and British Guiana.

MONTRICHARDIA Crueger: *M. arborescens* (L.) Schott is common in the coastal region of Suriname, its vernacular name being mokko-mokko. Sometimes its stems are spiny; these spiny specimens were regarded by G. W. F. MEYER and by SCHOTT as a distinct species: *M. aculeata* (G. W. F. Mey.) Schott, and by ENGLER as a variety: var. *aculeata* (G. W. F. Mey.) Engl. In our opinion this difference is of little value. We wish to draw the attention to what SIMMONDS has to say on this topic, however: "The variety *aculeata* (Mey.) Engl. differs from the typical plant in its greater height, spiny stems, rough petioles and the veins more exposed in the sinus. Field work in Grenada, B.W.I., suggested that the variety is a good one, though there is little difference in size and there is intergradation of spininess. A distinction is not normally possible in the herbarium however. It is possible that an ecological difference exists, the typical form preferring fresh water sides, the var. *aculeata* saline or at least brackish water, and it is desirable that this point should be observed by collectors."

The study of the material collected in Suriname showed that a second species exists with an area limited to the river banks of the interior districts i.e. along the upper reaches of the rivers. This species is characterized by the leaf shape, the nervation and the length of the cusp in which the leaf sheath goes out and appeared to be conspecific with *M. linifera* (Arr.) Schott, previously known from Southern Brazil.

Another species, *M. splitgerberi* Schott, was described from Suriname. According to ENDER, Ind. Ar. (1864), p. 55, it is a synonym of *M. arborescens* (L.) Schott. The type specimen, Splitgerber s.n., apparently has been lost and also the drawing preserved in the Vienna herbarium and cited by ENGLER in Das Pflanzenreich IV. 23C (1911), p. 125.

SCHISMATOGLOTTIS Zoll et Mor.: The most remarkable result of our studies of the Suriname *Araceae* was the finding of a new species of the chiefly Malesian genus *Schismatoglottis*. The specimen was collected by MAGUIRE in 1944 on Tafelberg Mt. but was not recognized by A. D. HAWKES, who listed it as *Dieffenbachia seguina* (L.) Schott. The present authors describe it as a new species: *Schismatoglottis americana* Jonk. et Jonk., nov. spec. (fig. 2).

Cataphylla membranacea lanceolata acuta. Foliorum petiolus teres, 13–26 cm longus, supra sulcatus, ad 11 cm longitudinis vaginatus. Lamina herbacea elliptico-oblancheolata, basi rotundata et ad petiolum subcontracta, apice acuminata, longe-subulata, 20–30 cm longa et 9–13 cm lata; subula circ. 2.5 cm longa; costa crassa; nervis lateralibus I utrinque circ. 6. Pedunculus teres, circ. 24 cm longus. Spatha basi obliqua, parte inferiore persistente, 3–3.5 cm longa. Spadix sessilis, basi adnatus. Ovarium ad 2 mm longum et 0.5–1 mm crassum, cylindricum, stigmatibus annulari sessili coronatum; ovula pauca placentis 2 parietalibus affixa. Semina 1–3, ovoidea, apiculata, 12-costata. Typus: Maguire 24289 in herbario NY—Surinamo in monte Tafelberg.

This is the first species of this genus recorded from America. Closely related however is the monotypic genus *Philonotion* Benth.; *P. spruceanum* Benth. was once collected at Rio Panuré, Amazonian Brazil (Spruce n. 2948). The leaves show the same characteristic nervation and the same distinct marginal vein and long cusp. The



Schismatoglottis americana
Jonk. & Jonk.

Fig. 2. a. fruiting plant, b. fruiting spadix, c. pistil, d. fruit, e. seed, f. horizontal section of seed.

shape of the leaf sheath and the stamens also agree. *Schismatoglottis* however has 2—4 parietal placentas, whereas *Philonotion* has a single parietal ovule in its unilocular ovary. Some species of *Schismatoglottis* provided with two parietal placentas in the ovary have but a small number of ovules viz. circ. 10. *S. americana* too has 2 parietal placentas

and but 4 ovules. This species is perhaps to be regarded as a link between the asiatic species of the genus, especially those provided with 2 parietal placentas and a small number of ovules, and the genus *Philonotion* from Amazonian Brazil characterized by a 1-celled ovary with a single parietal ovule. More material is needed, however, to decide whether the genus *Philonotion* should be sunk in *Schismatoglottis*.

These investigations have been carried out in the Botanical Museum and Herbarium of the State University of Utrecht, Netherlands (director: Dr J. LANJOUW). The authors wish to express their grateful thanks to the directors of the herbaria at Berlin, Brussels, Göttingen, Kew, München, Leiden, New York, Stockholm and Uppsala for the loan of herbarium specimens. A special word of thanks is due to the directors, keepers and staff of the herbaria and botanical gardens, personally visited by the authors, viz. at Amsterdam, Brussels, Gent, Kew, Leiden, London and Paris, for the hospitality and great assistance given during their stay.

Finally we wish to tender our most sincere thanks to Dr C. E. B. BREMEKAMP for his valuable help with the revision of the english text.

NOTES ON MALAYSIAN GRASSES III¹

BY

P. JANSEN (Amsterdam)²

(received June 12th 1953)

DEYEUXIA Clar. ex Beauv.

1. *Deyeuxia pseudopoa* nov. spec.—Fig. 1.

Perennis, caespitosa. Culmi erecti, inferne 3—4 mm crassi, fistulosi, glabri laevesque, usque ad 120 cm alti, nodis 4—6 obscuris; internodium superius 30—45 cm longum. Vaginae teretes, glabrae laevesque, striatae, angustae, quam internodia breviores. Ligula membranacea, glabra, 5 mm longa, acuta, magis minusve lacerata. Foliorum laminae lineares, planae, tenuiter nervatae, glabrae, marginibus scabrae, inferiores elongatae, usque ad 40 cm longae, 5—8 mm latae, superiores breviores. Panícula oblonga, 15—25 cm longa, erecta vel subnutans; rami divaricati, capillares, laeves, subflexuosi, in verticillis distantibus dispositi, infimi 4—5-nati, 6—8 cm longi, inferne nudi, supra medium iterum ramosi; ramuli scaberrimi. Pedicelli spiculas subaequant, scaberrimi, apice subincrassati. Spiculae virides, uniflorae, 4.5—5 mm longae, lanceolatae. Glumae inaequales, ambae acutissimae vel mucronatae vel brevissime aristatae, omnino scabrae, carina serrulato-scabrae; ima angusta, 2—3 mm longa, secunda subtrinervia, quam prima 1 mm longior. Callus pilis paucis brevissimis munitus vel glaber. Rhachilla in setam 1.5—2.5 mm longam manifeste producta. Lemma 4.5—5 mm longa, lanceolata, lateraliter valde compressa, indurata, punctulato-scabra, indistincte 5-nervis, carina in aristam 0.5—2 mm longam desinente. Palea quam lemma subbrevior, nervis 2 approximatis. Antherae ca. 1 mm longae. Caryopsis matura ignota.

Distr. Sumatra, Gajolands: summit of Goh Lembuh, Van Steenis 9135 (type); Mt Losir, Van Steenis 8660.

Ecol. High-mountain grass; along shaded brooks in the moss-forests, from 3000—3500 m altitude.

Note. This remarkable species has the habit of a large *Poa* and belongs to the small group of *Deyeuxia* species with the lemma longer

¹ Part I in Reinwardtia 2 (1953) in the press; part II in Act. Bot. Neerl. 1 (1953) 468—483.

² Honorary collaborator Flora Malesiana Foundation.



Fig. 1. *Deyeuxia pseudopoa* Jansen. a. Panicle, $\times \frac{1}{2}$, b. ligule, c. spikelet.

than the glumes, the callus very short-hairy and a bristle-like prolongation of the rhachilla, described by Miss J. W. VICKERY (1940). The shape and indurated texture of the lemma and the length of the awn is well within the generic range.

ERIANTHUS Michx.

1. **Erianthus velutinus** (Holtum) Jansen, nov. comb.

Spodiopogon velutinus Holtum in Gard. Bull. Sing. (1947) 297.

This species is nearly related to *E. beccarii* (Stapf) Jansen. It may be distinguished by the cuneate base of the blades, which are softly villous on the lower surface, by the hirsute sheaths, the whitish panicle and the perfect awn of the upper lemma.

FESTUCA L.

1. **Festuca nubigena** Jungh. — Fig. 2, 3.

This remarkable species was described by JUNGHUHN (1845). BUSE (1854) described it again after having studied Junghuhn's original specimens from Mts Lawu and Merbabu (Central Java). He stressed the typical habit: "Caespites ibi format insularum ad instar, vallibus 1—3 pedilibus segregatas". STEUDEL (1854) distinguished two species in Java: *F. nubigena* Jungh. and *F. nubila* Jungh. (in lit. ad Nees). Neither at Bogor nor at Leyden specimens of *F. nubila* are represented. According to St. YVES (1928), who saw a specimen of *F. nubila* in the Berlin Herbarium, the type of *F. nubila* shows only trifling differences with *F. nubigena* and he considered them to be conspecific. CHASE (1943) mentioned *F. nubila* from New Guinea, and remarked: "This species is closely related to *F. nubigena* but has taller culms, much longer leaves, larger lax panicles and larger spikelets with hispidulous glumes and lemmas". She based her opinion on the specimens collected by Brass and Meijer Drees in New Guinea. By courtesy of Dr R. J. Swallen I could study these Brass specimens of the U. S. Nat. Herb. and compare them with a duplicate set of Brass & Meijer Drees in the Rijksherb. Leyden, in which Herbarium are also deposited numerous specimens of *F. nubigena* from the mountains of Java and Lombok.

The latter specimens possess the following characteristics:

- a. *F. nubigena* is a densely caespitose perennial with numerous long-leaved, closely packed, intravaginal innovations, surrounded by the broadened old sheaths and building separate and distant tussocks.
- b. The sheaths of the innovations are entire for the largest part (up to 2/3) and in the upper portion of the entire part they are very thin and implicate sulcate. In the opinion of St. Yves and De Litardière this is a character of major importance bringing the species in the group of *F. amethystina* L.



Fig. 2. *Festuca nubigena* Jungh. *a.* Type from Java, $\times \frac{1}{2}$, *b.* spikelet, *c.* lemma and palae.

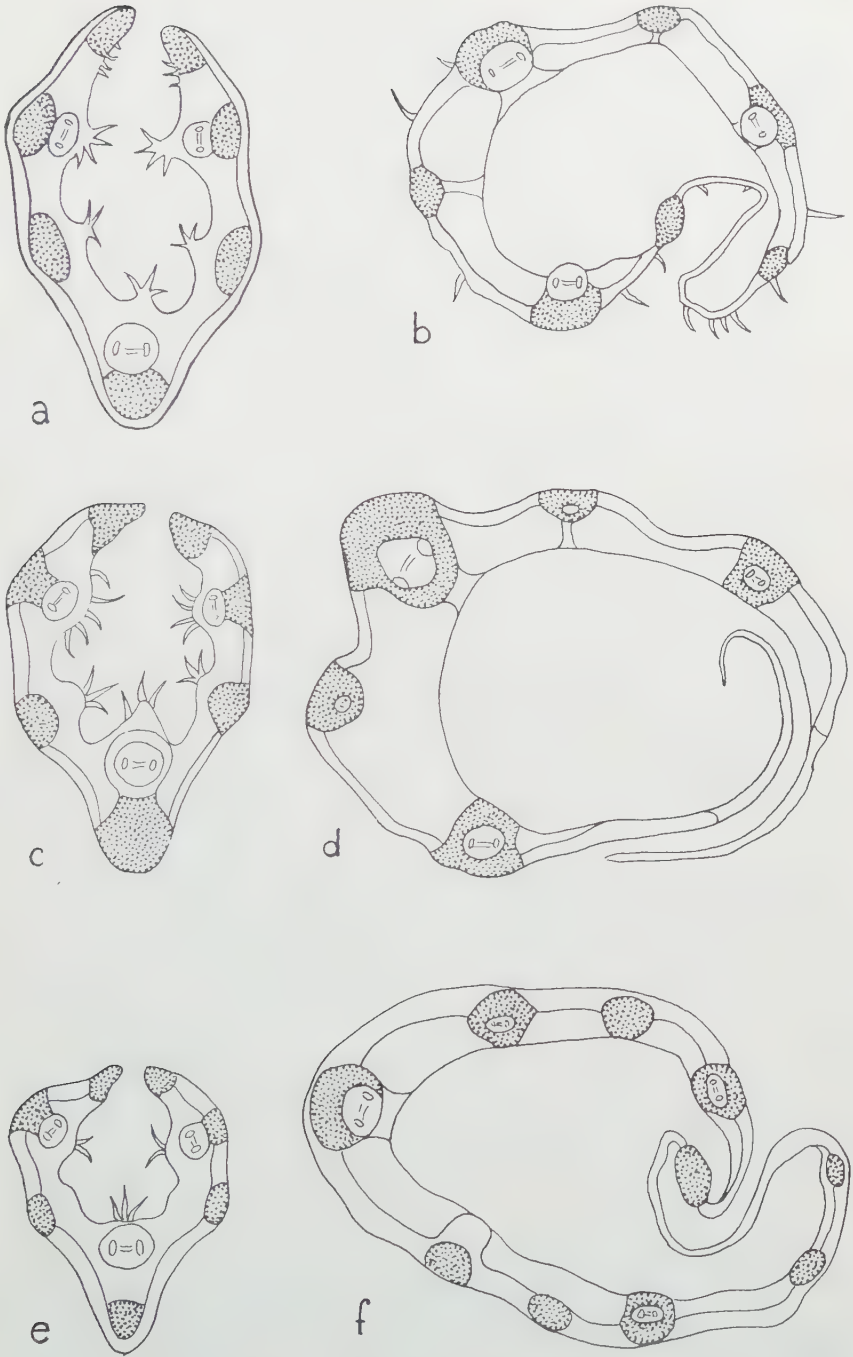


Fig. 3. *Festuca nubigena* Jungh. Transverse sections of blades and sheaths: a/b. Zollinger 3967 (Java), c/d. Junghuhn (Java), e/f. Elbert 2238 (Lombok).

- c. The innovation-blades are setaceous involute, usually 20—40 cm long, glabrous and smooth at the outer side, with some minute hairs at the inner side, 0.6—0.7 mm in diameter, usually 3-, more rarely 5-nerved. In transverse section the vascular bundles are supported by sclerenchym only at the lower side of the bundles, with a small layer of sclerenchym at the apices of the margins. In this respect they differ from the figures given by St. YVES (1927). They resemble most his f. 102. When we take the description of St. YVES (1928) as a base, then the specimens from Java and the Lesser Sunda Islands might be separated as a distinct variety.
- d. The culms are elegant, thin, glabrous and smooth below the panicle, up to 0.75 m high.
- e. The panicle is 8—20 cm long, more or less contracted and often somewhat drooping, the 1—3-nate branches rather short with few spikelets. The axis of the panicle, the branches, branchlets and pedicels are antorsely scabrid to hispid or more rarely setose.
- f. The spikelets are 3—5—(7)-flowered, 7—10 mm long, with the upper floret male. The glumes are unequal, acuminate to minutely awned, the first 3.5—5 mm long and 1-nerved, the second 5—6 mm long and 3-nerved, both scaberulous towards the apex. The joints of the rhachilla are rather long, 1.5—2 mm, and finely but distinctly hairy (an important character of this species and the related ones). The lemmas are 6—7 mm long, lanceolate, with an entire tip, 5-nerved, usually granulate over the whole surface, more or less hispid on the margins and towards the tip. The awn is straight, rather solid and finely hispid, usually 4—5 mm long. The shortly bidentate palea is usually longer than or rarely as long as the lemma. The linear anthers are up to 4 mm long. The ovary is glabrous or with a few short bristles at the tip.

The New Guinean material, cited above, is a mixture of various species and forms. The collected tufts have been torn in fragments and these have been distributed, hence many herbarium specimens do not possess any innovation. Pressed and mounted on the sheets some of the shoots make the impression of being extravaginal, but stoloniferous culms are out of question. The old sheaths are often weathered. In general the specimens are more hairy and the variation of this indumentum is considerable. The blades are often shorter and wider and the culms are lower. They have been collected between 3200 and 4050 m altitude in wet localities.

- a. Brass 4204 (U. S. Nat. Herb. 1614466), Mt Alb. Edward at 3680 m altitude.

This specimen of *F. nubigena* is more or less similar to the Javan specimens. The old sheaths are wanting, probably weathered away. The innovation-sheaths are nearly entire, in the upper closed part deeply implicate-sulcate. The blades are long, narrow, 3-nerved, smooth and glabrous. The spikelets are more purplish than usual, the lemmas granulate to minutely scabrid.

- b.* Brass & Meijer Drees 9845 differs by the blades, which are clothed with rather long hairs on both surfaces, and by the very dark, quite purple spikelets with minutely hairy lemmas. Brass & Meijer Drees 9823 is a very loosely caespitose form. The old sheaths are wanting and the separate bundles of culms and innovations give the impression of extravaginal growth. Both numbers have been collected on Mt Wilhelmina, at 3560 m altitude.

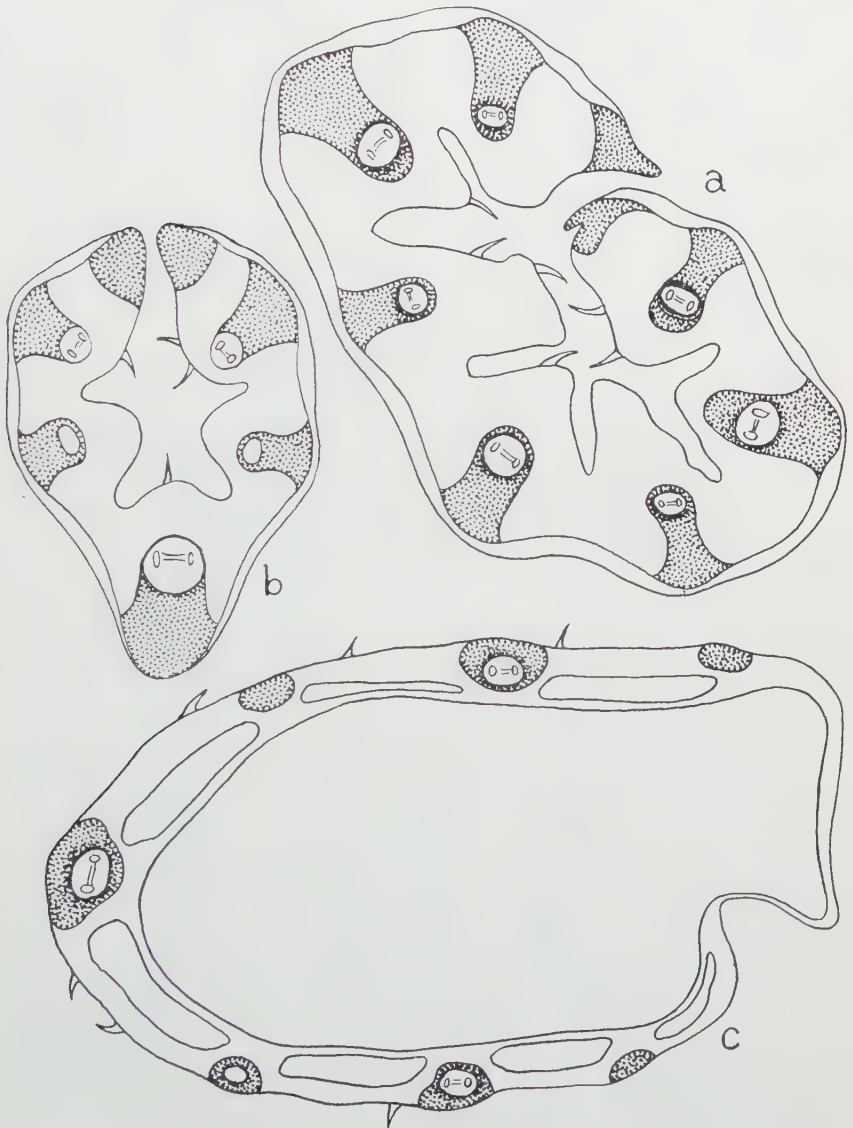


Fig. 4. *Festuca nubigena* Jungh. ssp. *novoguineensis* Jansen. Transverse sections of blades: *a.* Brass 9976, *b.* Brass 10066; *c.* transverse section of sheath, Brass 10066.

- c. The other specimens of *F. nubigena* from New Guinea differ by the wider 5—7-nerved and usually shorter and more stiff blades, the firmer culms, woolly hairy below the panicle, the spike-like panicle, the adpressed short and few-spikeled branches, and the usually densely pubescent lemmas. I propose to call them

ssp. **novoguineensis** nov. ssp. — Fig. 4.

Laminae modice latiores quam in var. *nubigena*, 5—7-nerviae. Culmi firmiores, infra paniculam lanati. Panícula spiciformis, ramis brevibus, adpressis, spiculas paucas gerentibus.

Distr. Mt Wilhelmina, at 3660 m altitude, alpine grassland, covering marshy hollows, Brass & Meijer Drees 9976, type in U. S. Nat. Herb. 1761722; Lake Habbema at 3225 m altitude, sandy banks of a small stream, Brass 9325 in U. S. Nat. Herb.

The following specimens differ from those cited above by the much shorter, more stiff blades, less than 20 cm long and the still more contracted and shorter panicle:

Lake Habbema at 3225 m altitude, scattered over a wet peaty flat, Brass 9547.

Mt Wilhelmina at 3400 m altitude in a rather wet grassy valley, Brass & Meijer Drees 9747.

Mt Wilhelmina at 4050 m altitude, on shallow wet soil of old screes, Brass & Meijer Drees 10066.

The height of the culms decreases with the altitude.

2. **Festuca parvipaleata** nov. sp. — Fig. 5, 6.

Gramen perenne, dense caespitosum, innovationibus intravaginalibus, plerumque vaginis vetustis basi latioribus inclusum. Culmi erecti, glabri vel subglabri, 40—70 cm alti. Innovationum vaginae in parte quarta inferiori integrae, in parte superiore fissae et apertae, modice latae. Ligula membranacea, 3—4 mm longa, breviter auriculata. Laminae lineares, involutae vel setaceae, apice acuto, 25—40 cm longae, 0.7—1 mm in diam., 5-nerviae, utrinque pubescentes vel demum inferne glabrescentes; laminae foliorum caulinarum valde breviores et paullo latiores. Sectio transversa foliorum innovationum demonstrat fasciculos fibrovasculares utroque cum superficiebus per fasciculos sclerenchymaticos connectos, etiam marginibus foliorum fasciculos sclerenchymaticos continentibus. Panícula 8—12 cm longa, axi, ramis et pedicellis scabris vel minute pilosis. Rami inferiores 1—3-nati, fere patentes, 3—5 cm longi, superiores solitarii vel binati, breviores. Spiculae 8—10 cm longae, plerumque 5-florae, virides vel purpureae, supra pedicello variabilis longitudine positae. Glumae inaequales, apicem versus scabrae. Gluma prima acuta, 3—4 mm longa, 1-nervia; gluma secunda latior, 6—7 mm longa, 3-nervia, acuta vel subulata. Internodia rhachidis 1—1.2 mm longa, dense minute pilosa. Lemma lanceolatum, valde 5-nervium, un aristam 2—3 mm longam scabridam rectam attenuatum, lemma flosculorum inferiorum 8—9 mm longum, superiorum gradatim brevius, glabrum vel nervis magis minusve pubescens. Palea quam lemma valde brevior. Antherae 2—2.5 mm longae. Apex ovarii glaber vel pilis paucis brevibus praeditus.

Distr. New Guinea: northern slopes of Mt Wilhelmina at 4050 m altitude, common in grass cover of old screes, Brass & Meijer Drees 10061, type in U. S. Nat



Fig. 5. *Festuca parvipaleata* Jansen. *a.* Type from New Guinea (Brass 10061)
 $\times \frac{1}{2}$, *b.* spikelet, *c.* lemma and palea.

Herb. 1761726. From the same locality: Brass & Meijer Drees 10070 & 10071, slightly differing in the blades being very hairy on the outer surface.

This species has more or less the same habit as *F. nubigena* but differs in a character of paramount importance: its sheaths are only entire up to $1/4$ of their length, then split and open, while in *F. nubigena* the sheaths are nearly entire to the tip and in their upper part deeply and implicate sulcate. A second remarkable character is furnished by the short palea, about $2/3$ as long as its lemma, while in *F. nubigena* the palea is as long as or longer than its lemma.

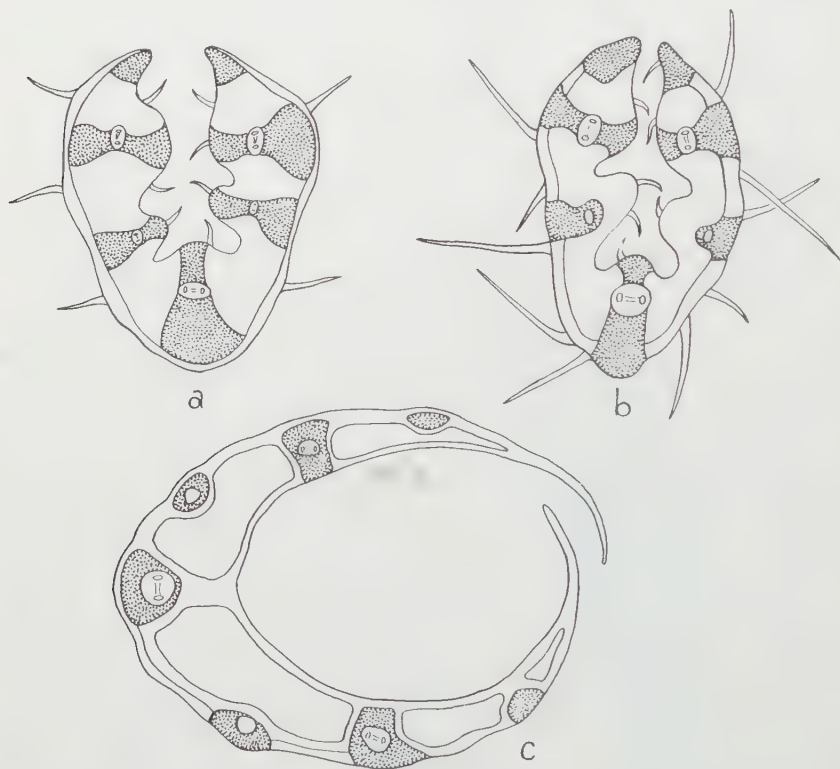


Fig. 6. *Festuca parvipaleata* Jansen. Transverse section of blades: *a.* Brass 10061, *b.* Brass 10071; *c.* transverse section of sheath, Brass 10071.

3. Brass & Meijer Drees 9128, 9715 & 9824, from New Guinea, certainly represent a new species. The sheaths bear a number of different forms. The culm-blades are 9-nerved; the culms are slightly pilose; the panicle is large with long spreading branches; the spikelets are large, up to 1 cm long; the lemmas are densely and hispidly hairy all over; the palea is as long as the lemma; the joints of the rachilla are finely hairy. As the innovations are wanting I refrain from naming it.

4. ***Festuca papuana*** Stapf in Kew Bull. (1899) 117. — Fig. 7. This species is characterized by its erect, setaceous convolute,

rigid and pungent blades, in transverse section tricostate, the vascular bundles not supported by sclerenchym, the short contracted panicle, the purplish to black spikelets, the subequal glumes and the prominently 5-nerved lemmas tapering into a short awn.

Stapf (l.c.) supposed that the "*Festuca ovina*" mentioned by F. v. MUELLER (1889) also belonged to *F. papuana*. In Herb. Melbourne I saw the specimens collected by MacGregor on Mt Knutsford and the Owen Stanley Range. They certainly represent *F. papuana*.

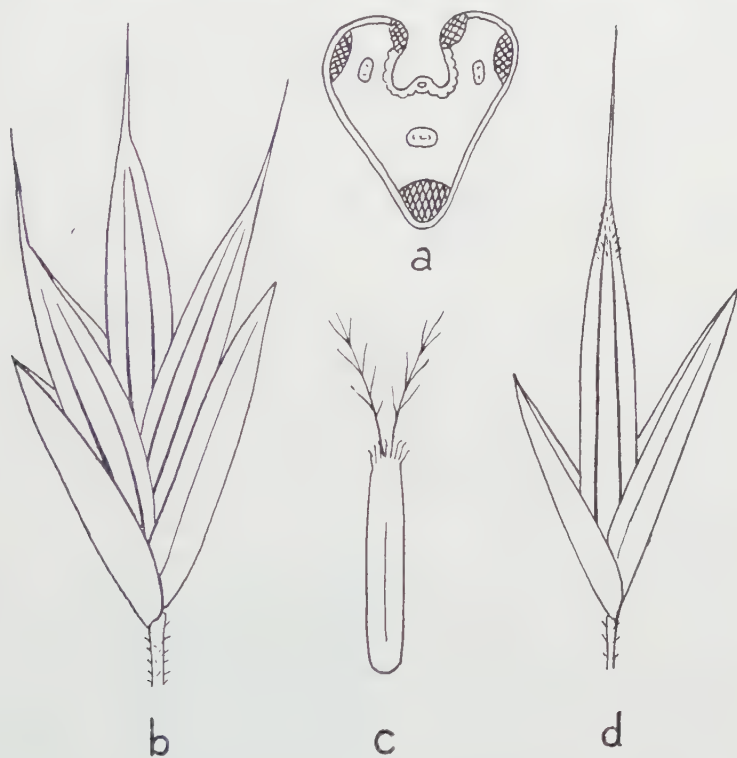


Fig. 7. *Festuca papuana* Stapf. a. Transverse section of blade, b. spikelet, c. ovary, d. spikelet of var. *monantha* (Stapf) Jansen.

STAPF (1899) described also *Festuca monantha* from Mt Scratchley. I saw the type in Herb. Kew. Stapf separated it from *F. papuana* by the sheathed shorter culms, the 1-flowered spikelets, and the apex of the ovary bearing some short hairs. Using a strong lens I found that the apex of the ovary in *F. papuana* also bears some short bristles. As the other differences are trifling it seems advisable to consider it a 1-flowered variety of *F. papuana*: ***F. papuana* Stapf var. *monantha* (Stapf) Jansen, nov. comb.**

5. ***Festuca sumatrana* Jansen, nov. sp. — Fig. 8.**

Gramen perenne, dense caespitosum, innovationibus intravaginalibus. Culmi erecti, 20—30 cm alti, teretes, glabri laevesque.

Innovationum vaginae fere ad basin usque fissae et apertae, apice breviter auriculatae. Ligula brevissima, truncata. Foliorum lamina linearis, modice rigida, 7—9-nervis, convoluta vel secundum margines tantum involuta, 6—10 cm longa, 3—3.5 mm lata (explanata), abruptiuscule argute acutata, glabra; sectione transversa stratum angustum interruptum sclerenchymae subepidermalis exhibens, basi 7—9 fasciculis vascularibus auctum, apice fasciculis sclerenchymatosis parvis munitum. Paniculae 6—8 cm longae; rhachis angulosa, minute scabrida, magis minusve flexuosa. Rami solitarii vel gemini, divaricati; infimi 3—4 cm longi, superiores gradatim breviores. Pedicelli crassiusculi, minute scabri, 4—6 mm longi. Spiculae virides, glabrae, 4—5-florae, \pm 9 mm longae (aristis haud computatis). Glumae valde inaequales; infima \pm 3 mm longa, uninervis; secunda 6—7 mm longa, quam prima latior, 3-nervis; ambae rigidae, acutissimae. Rhachillae internodia \pm $\frac{1}{2}$ mm longa, glabra. Lemmae glabrae, laeves, inconspicue nervatae, attenuatae in aristam 3—6 mm longam, rectam vel subflexuosam. Antherae $\frac{1}{2}$ mm longae et fere aequae latae. Ovarii apex glaber.

Distr. Sumatra, Atjeh, East slope of Mt. Kemiri, in small dense tufts among rocks at 3300 m altitude, Van Steenis 9629. Type in Rijksherb. Leyden 952—64—404.

This species is characterized by its dense small tufts, the rather wide, not setaceously but slightly inrolled 7—9-nerved blades, the short culms, the wavy panicle-axis, the thick and rather long pedicels, the very unequal stiff glumes, the short glabrous joints of the rhachilla, the indistinctly nerved smooth lemmas, the short nearly square anthers and the glabrous tip of the ovary.

KEY TO THE MALAYSIAN SPECIES OF FESTUCA

1. Blades 7—8 mm wide, flat and soft with an obtuse or rounded base. Awn of the lemma 10—11 mm long, tender and flexuous. **F. leptopogon** Stapf
1. Blades much narrower, 0.6—3 mm wide, inrolled to setaceous. Awn of the lemma less than 6 mm long, straight.
 2. Joints of the rhachilla glabrous and less than 1 mm long. Blades stiff, very acute, usually shorter than 10 cm. Panicle 6—8 cm long, the axis and branches glabrous, smooth or slightly scabrous.
 3. Blades 0.6—0.7 mm in diameter, setaceous. Panicle-branches adpressed to the axis. Spikelets purple to black. Glumes subequal, 4 and 5 mm long. Tip of the ovary minutely hispid. **F. papuana** Stapf
 3. Blades about 3 mm wide when flattened out, slightly inrolled. Panicle-branches spreading. Spikelets green. Glumes very unequal, 3 and 6—7 mm long. Tip of the ovary glabrous. **F. sumatrana** Jansen
 2. Joints of the rhachilla finely hairy and much longer. Blades up to 40 cm long, softer. Panicle 10—20 cm long, often somewhat nodding; the axis, branches branchlets and pedicels scabrous to hispid or setose.

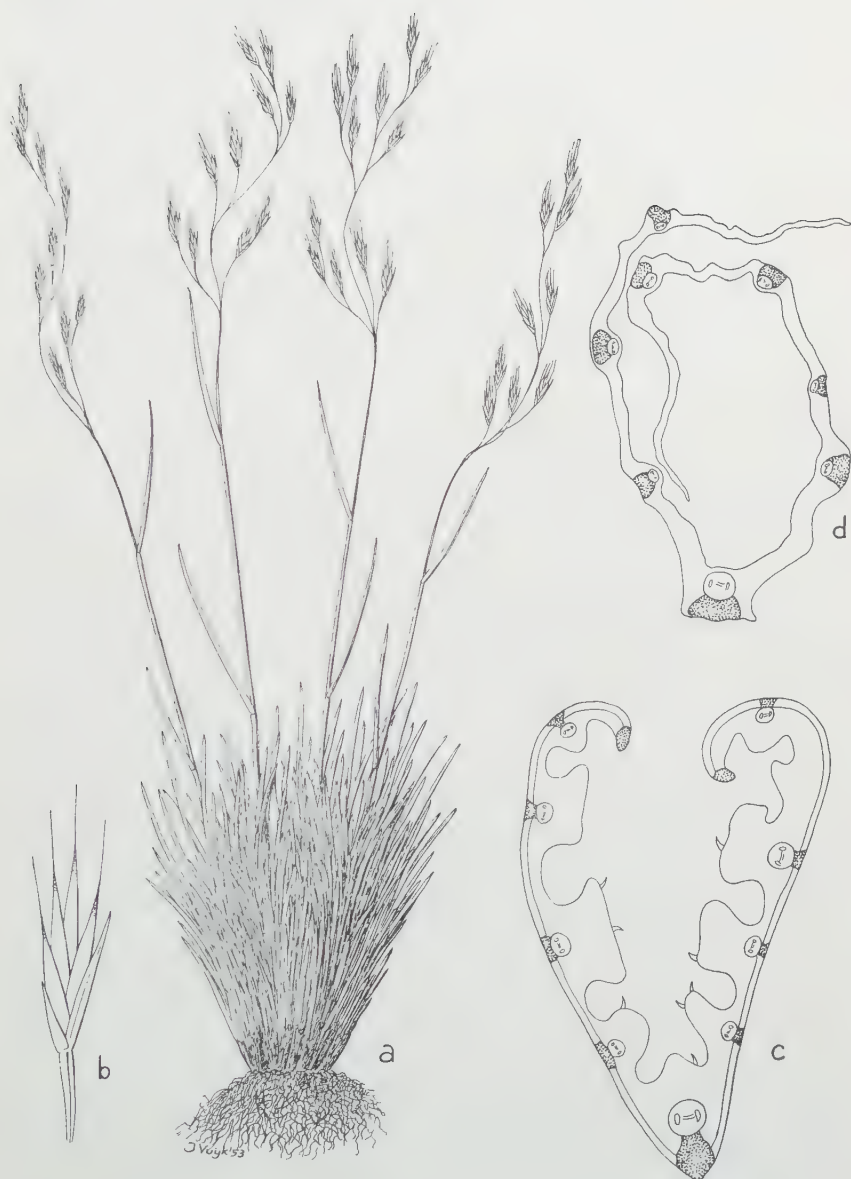


Fig. 8. *Festuca sumatrana* Jansen. *a.* Type, $\times \frac{1}{2}$, *b.* spikelet, *c.* transverse section of blade, *d.* transverse section of sheath.

4. Sheaths of the innovations entire for the largest part, in the upper portion of the entire part deeply implicate-sulcate. Palea longer than or rarely as long as the lemma.

F. nubigena Jungh.

4. Sheaths of the innovations split and open, only entire in the lower $1/4$. Palea $1/2$ — $2/3$ as long as the lemma.

F. parvipaleata Jansen

GARNOTIA Brongn.

In DUPERREY (1830) Brongniart described this genus with *Garnotia stricta* from Tahiti as the only species. Neither the type nor any other authentic specimen has been available to later authors. In Malaysian literature *G. stricta* Brongn. was misinterpreted and the name was commonly used for all the *Garnotia* specimens collected within the Archipelago.

EVEN BACKER (1928) still used this name for the Javan specimens, although MERRILL (1906) already doubted the determination. He stated, that the Philippine form of *Garnotia* might be a distinct species, characterized by the long-awned lemma. KNEUCKER (1909) published *G. stricta* var. *longiseta*, accredited to Hackel and based on the manuscript name *G. longiseta* Merr.

Later some new species were published from New Guinea: *G. ledermannii* Pilger in Bot. Jahrb. 52 (1914) 171, *G. mezii* Janovsky in Fedde, Repert. 17 (1921) 86, and *G. papuana* Ohwi in Bot. Mag. Tokyo 56 (1942) 1.

Recently J. V. Santos started monographic research of the genus. He published *G. mindanaensis* in J. Wash. Ac. Sc. 33 (1943) 135, *G. caespitosa* in J. Arn. Arb. 25 (1944) 89, and *G. philippinensis*, l.c. 94. Finally Ohwi described *G. spadicea* in Bull. Tokyo Sc. Mus. 18 (1947) 9 from Sumatra.

The "Revision of the genus *Garnotia*" by SANTOS (1950) includes 73 species, 46 varieties and 24 forms, among which 11 species from Malaysia. The distinctions are very fine, many of the microspecies and varieties are based on one specimen only. For example Santos has seen 6 specimens of *G. fragilis* and everyone of them belongs to a separately named variety. He lays stress on many minor differences, e.g. the tip of the lemma, being quite entire and tapering into the awn, or awned between the minute teeth of a bidentate tip. His interpretations may be right, but such a character is difficult to observe: the apex of the lemma is very thin and fine, and often tears in drying, with the result that in a single panicle both kinds of lemmas may be present. A similar difficulty is connected with the characters of the glumes, being emarginate or not. The notch, if present, is often so minute or variable, that it hardly seems to be a reliable character fit to separate species. The key, including all his species, varieties and forms has become so very intricate, that the author was obliged to place the same species (*G. ledermannii*) into 2 different series of the subsection *Longiaristatae*.

KEY TO THE MALAYSIAN SPECIES OF GARNOTIA

1. Spikelets 6—7 mm long, brown. Panicle short, stiff, spike-like. Blades rigid and thick 1. **G. spadicea**
1. Spikelets 3—4.5 mm long, green. Panicle loose and usually much longer. Blades soft, flat or involute.
 2. Lemmas quite awnless. Glumes awnless to very minutely mucronate. Branches of the panicle less than 5 cm long. Spikelets 4—4.5 mm long. 2. **G. philippinensis**
 2. Lemmas distinctly and usually long-awned.
 3. Awn of the lemma perfect, geniculate with a twisted column and a flexuous subule.
 4. Culms simple, 30—60 cm high, erect with pubescent nodes. Blades lanceolate, up to 12 mm wide, flat, papillose-pilose. Both glumes emarginate at the tip. (Lemma awned between the minute teeth of the bidentate tip) 3. **G. fragilis**
 4. Culms tender, about 20 cm high, freely branching at base. Blades linear-lanceolate, 2—4 mm wide, sub-involute, glabrous to minutely and sparsely pilose. First glume entire, second emarginate at the tip. (Lemma awned from the entire tip).
 4. **G. pahangensis**
 3. Awn of the lemma straight, flexuous or tortuous, neither geniculate nor twisted.
 5. Awn of the lemma strongly attenuate towards the tip, flexuous and tortuous. Basal hairs inconspicuous of wanting.
 6. Spikelets 4—4.5 mm long. Basal hairs inconspicuous. Nodes of the culm pubescent. Branches of the panicle loosely adpressed. (Lemma awned from the entire tip) . . . 5. **G. mindanaensis**
 6. Spikelets 2.5—3.8 mm long. Basal hairs wanting. Branches of the panicle more spreading. (Lemma awned between the teeth of the minutely bidentate tip).
 7. Culms rather robust, up to 80 cm high. Panicle up to 40 cm long, the branches in whorls and bearing many spikelets. Blades sparsely puberulent from the middle of the tip. Glumes subequal, about as long as the spikelet 6. **G. mezii**
 7. Culms slender, decumbent and rooting at the lower nodes. Panicle less than 10 cm long, the few 1-nate distant branches with few spikelets. Blades sprinkled with long tubercle-based hairs. Glumes very unequal.
 7. **G. ledermannii**

5. Awn of the lemma moderately attenuate towards the tip, straight or subflexuous. Basal hairs more or less copious, 0.5—0.7 mm long. Spikelets 3—3.5 mm long.
8. Ligule very short, less than 0.5 mm long. Blades flat to convolute when dry, up to 30 cm long, usually pubescent on both surfaces. Nodes of the culm pubescent. Spikelets narrow, about 0.5 mm wide. Culms strongly branching at the base, building dense tufts. 8. ***G. acutigluma***
8. Ligule 1—1.7 mm long. Blades involute, suberect, 7—10 cm long, glabrous. Nodes of the culm glabrous. Culms simple. Spikelets lanceolate, 0.7 mm wide.

9. ***G. erecta***

1. ***Garnotia spadicea*** Ohwi in Bull. Tokyo Sc. Mus. 18 (1947) 9. — Fig. 9.

This rigid mountain species differs from all other Malaysian ones by the 6—7 mm long brown spikelets, the narrow short strict panicle, and the rigid, thick, 3—9 cm long, loosely convolute blades.

Distr. N. Sumatra, Gajo Lands, Mt Losir, 2200—2800 m altitude, Van Steenis 8479 & 8539.

2. ***Garnotia philippinensis*** Santos in J. Arn. Arb. 25 (1944) 94.

Characterized by its awnless lemmas and awnless to very minutely mucronate glumes, the short panicle-branches, and the 4—4.5 mm long spikelets.

Distr. Santos only mentions a single specimen from the Philippines (Ramos, B. S. 42963). I also saw specimens from Celebes (Kjellberg 3042) in Herb. Bogor and from New Guinea (Zippel a. 1828) in the Rijksherb. Leyden. In the specimens from Celebes the nodes of the culms are nearly glabrous, the blades are narrower and loosely involute towards the tip, and the spikelets are nearly nude at the base.

3. ***Garnotia fragilis*** Santos in J. Arn. Arb. 25 (1944) 89.

This is one of the few species with a perfect, geniculate awn, the column twisted and the subule flexuous. Spikelets 4—4.5 mm long. Blades of the basal leaves short (3—4 cm), those of the culm-leaves 6—10 cm by 7—9 mm, lanceolate, flat, sprinkled with tubercle-based hairs.

Distr. India to Malaysia.

SANTOS (1950) cited six specimens, every one of them bearing a separate varietal name. I only examined the Malaysian varieties:

var. *parcitorita* Santos l.c. 132.

The specimen in Herb. Kew. (Malay Peninsula, Haniff 638) differs only slightly from the description and figure of the type variety in having the column of the awn somewhat less twisted.

var. *brevifolia* (Ohwi) Santos l.c. 132, based on *Garnotia brevifolia* Ohwi in Bull. Tokyo Sc. Mus. 18 (1947) 9.

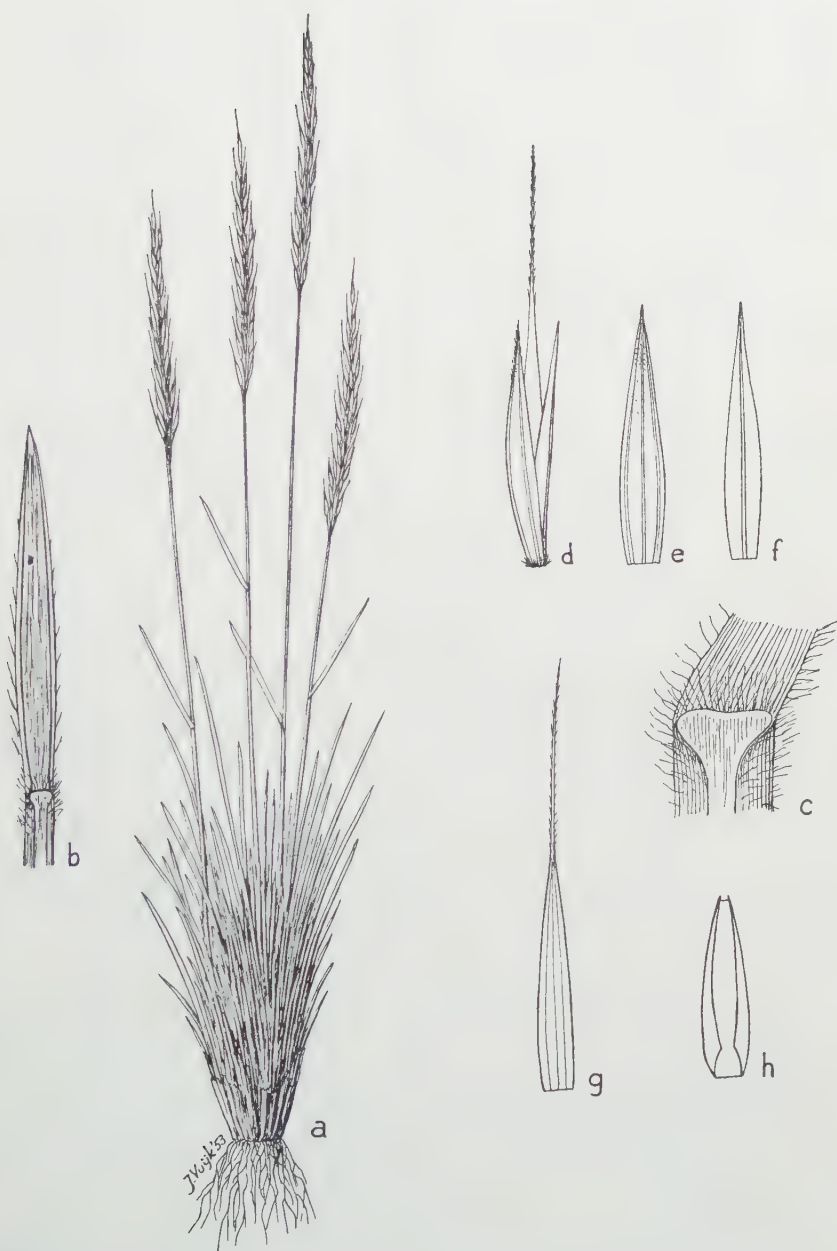


Fig. 9. *Garnotia spadicea* Ohwi. *a.* Type, $\times \frac{1}{2}$, *b.* culm-blade, *c.* ligule, *d.* spikelet, *e.* first glume, *f.* second glume, *g.* lemma, *h.* palea.

Santos studied an isotype (Java, Bakhuizen van den Brink 4687). I saw the type-specimens in Herb. Bogor.; they differ slightly mutually. One of them has the culm strictly erect like in *G. fragilis* var. *fragilis*, the other specimen on the same sheet has the culm slightly decumbent at the base. In both specimens the glumes are entire or minutely emarginate in a single panicle. In the youngest specimen the branches of the panicle are less spreading than in the other one.

These differences seem too trifling to split up the species into varieties.

4. **Garnotia pahangensis** Santos in Nat. & Appl. Sc. Bull. 10 (1950) 133.

This is also a species with a perfect, geniculate awn. Santos cited one specimen from Pahang (Seimund 435). I saw it in Herb. Kew. It resembles a reduced form of *G. fragilis* with tender short culms, but the blades are much narrower and subinvolute. According to Santos the first glume is entire, the second emarginate at the tip, while in *G. fragilis* both glumes are described as emarginate. It is very difficult to verify this character, as the specimen is glued to the sheet.

5. **Garnotia mindanaensis** Santos in J. Wash. Acad. Sc. 33 (1943) 135; in J. Arn. Arb. 25 (1944) 93.

This certainly is a good species, restricted to the Philippines and known from many localities. It is easily distinguished by the long, wide and flat blades, the long, narrow, interrupted panicle, and by the long awn of the lemma, straight to about the middle, then becoming strongly attenuate, capillary and tortuous towards the tip (the tortuous part sometimes drooping or caducous at maturity).

Santos in his Revision p. 98 proposes the combination *G. mindanaensis* var. *longiseta* (Hack.) Santos for specimens with smaller spikelets, only 3—3.75 mm long. The varietal epithet, though inappropriate, was used by Hackel in 1909 to separate these specimens from the awnless *G. stricta*.

6. **Garnotia mezii** Janovsky in Fedde, Repert. 17 (1921) 86.

This species is only known from New Guinea and seems rather variable. In general the culms are rather robust, the panicle is up to 40 cm long, with distant fascicles of branches, variable in length. The basal hairs of the spikelets are wanting or extremely short. The glumes are subequal, both distinctly 3-nerved; veins scabrous, inter-venium smooth. Lemma is as long as the spikelet. Awn straight in the lower part, thin and flexuous in the upper part.

The specimens I saw are very variable as to the length of the spikelets. The type-specimen (Schlechter 19542) has spikelets 2.5—2.8 mm long, in Clemens 4878 they are 4.7—5 mm long. The spikelets of the other specimens examined are intermediate in length.

SANTOS (1950, p. 92—93) distinguishes 4 varieties which I cannot accept. On the whole it appears to me that a final conclusion on

specific delimitation in this genus has to be postponed until additional material will be available. The attempt by Santos appears to be premature and unsatisfactory and to be mainly based on artificial distinction by measuring details.

7. **Garnotia ledermannii** Pilger in Bot. Jahrb. 52 (1914) 171; Santos in Nat. & Appl. Sc. Bull. 10 (1950) 99.

This species is only known from New Guinea: Kaiserin Augusta River, at 1400-1500 m altitude, forming a growth on high, steep, wet rock walls. The type was destroyed during the war. We are dependent on Pilger's description. The species seems to be related to *G. mezii*, but it is much more slender, decumbent and rooting at the lower nodes. Panicle less than 10 cm long with few, solitary, distant branches. Glumes unequal, 2.5 and 3.5 mm long. Awn strongly attenuated towards the tip and rather flexuous.

8. **Garnotia acutigluma** (Steud.) Ohwi in Bot. Mag. Tokyo 55 1941 393.—*Urachne acutigluma* Steud. Syn. 1 (1854) 121.—*Streptachne indica* Buse in De Vriese, Pl. Ind. Bat. Or. (1856) 99.—*Garnotia stricta* (non Brongn.) Merr. in Philip. J. Sc. 15 (1919); En. Born. Pl. (1921) 50; En. Philip. Pl. 1 (1923) 81; Backer, Handb. Fl. Java 2 (1928) 207.—*Garnotia papuana* Ohwi, in Bot. Mag. Tokyo 56 (1942).—*Garnotia caespitosa* Santos in J. Arn. Arb. 25 (1944) 92.

This is the species that has been repeatedly reported in the Malaysian literature as *G. stricta* Brongn. SANTOS (1944), guided by the original description and the plate of Brongniart, came to the conclusion, that the only specimens which might be recognized as illustrative were those of P. Nelson 359 & 480. Afterwards, in his Revision (1950, p. 53, 54) he refers the Nelson specimens to *G. stricta* var. *marianarum* Santos. For the Philippine specimens he proposed the name *G. caespitosa* Santos and for those from Java etc. he followed Ohwi, calling them *G. acutigluma* (Steud.) Ohwi.

After having studied numerous Malaysian specimens, I cannot agree with him. On comparing his key with his descriptions, I found that the varieties he distinguished merge into each other and often even overlap as to their characteristics. I cannot find a single reliable differential character. For instance in the key he states:

Spikelets 3—3.5 mm long **G. caespitosa**
Spikelets 3.75—4 mm long **G. acutigluma**

but in the former species he describes a var. *longiuscula* having spikelets of a length of 3.7—4 mm.

In his descriptions he states:

Lemma awned from the entire tip **G. caespitosa**
Lemma awned between the teeth of the shortly bidentate tip
G. acutigluma

but in the latter species he describes a var. *aberrans* with the lemma awned from the entire tip, &c.

It seems better to consider *G. caespitosa* a synonym of *G. acutigluma*.

Another microspecies is *G. longiaristata* SANTOS (1950, p. 70) from Borneo and the Philippines. The only difference with *G. acutigluma* consists in the longer awned glumes. This character is rather variable and not sufficient to delimit a new species.

I propose to name it: *G. acutigluma* var. *longiaristata* (Santos) Jansen, nov. comb.

9. **Garnotia erecta** Santos in Nat. & Appl. Sc. Bull. 10 (1950) 73.

This species differs from the preceding in the glabrous nodes, the glabrous blades with a ligule longer than 1 mm, and the lanceolate, slightly gaping spikelets. I only saw the type specimen in Herb. Kew. (S. F. 13854 from Pahang). Some other specimens are mentioned from Malaya and Indo-China. It may be a good species.

HYPARRHENIA Anderss.

1. **Hyparrhenia filipendula** (Hochst.) Stapf, Fl. Trop. Afr. 9 (1919) 322.

The Malaysian specimens belong to
var. **lachnathera** (Benth.) Jansen, nov. comb. — *Andropogon lachnatherus* Benth. Fl. Austr. 7 (1878) 534. — *Andropogon filipendulus* Hochst.
var. *lachnatherus* (Benth.) Hack. Monogr. Androp. (1889) 635; Merr. En. Philip. Pl. 1 (1923) 44.

Peduncle of the racemes at length longer than the spathes. Spikelets long and densely whitish villous. Racemes with one pair of homogamous and usually one pair of heterogamous spikelets.

Distr. Malaysia: Philippines, Celebes.

The number of heterogamous pairs of spikelets in the racemes is not constant, even in the same panicle. The form described as f. *bispiculata* Hackel in Philip. J. Sc. 1 (1906) Suppl. 267 hardly deserves distinction and may better be neglected.

ISCHAEMUM L.

1. **Ischaemum aristatum** L. Sp. Pl. (1753) 1049; Fischer in Kew Bull. (1935) 144. — *Ischaemum ciliare* Retz. Observ. 6 (1791) 36.
var. **scrobiculatum** (Wight & Arn.) Jansen, nov. comb. — *Ischaemum scrobiculatum* Wight & Arn. ex Steud. Syn. 1 (1854) 373.

Lower half of the first glume flatter than in the type and slightly wrinkled, the wings in the upper part less developed. Pedicelled spikelets shortly awned to awnless.

Distr. Malay Peninsula: Kedah, S. F. 25882 (Herb. Singapore).

ISEILEMA Anderss.

1. **Iseilema minutiflorum** spec. nov. — Fig. 10.

Gramen annuum. Culmi erecti, graciles, teretes, glabri, 2—3 dm



Fig. 10. *Iseilema minutiflorum* Jansen. *a.* Type, $\times \frac{2}{3}$, *b.* culm-blade, *c.* spathe, *d.* raceme with involucre spikelets, *e.* sessile spikelet, front view, *f.* sessile spikelet, back view, *g.* pedicelled spikelet.

alti. Vaginae saepe ad basin culmi aggregatae, compressae et carinatae, carina glanduloso-punctata scabrida. Ligula brevis, truncata, ciliata. Laminae lineares, acutae, planae vel conduplicatae, ceterum glaberrimae, usque ad 12 cm longae, si explanatae 2—2.5 mm latae, eae foliorum culmorum marginibus basin versus pilis gracilis mox deciduis ad basin tuberculatis praeditae. Inflorescentia foliacea, angusta, elongata, 15—20 cm longa, 4—5-nodis; internodium inferius usque ad 6 cm longum, superiora gradatim breviora, glaberrima et laevia; vaginae eae 8—12 mm longae, herbaceae, striatae, carina parce glandulifera. Spathae lanceolatae, acutae, tenuiter nervosae, marginibus late hyalinis, 6—8 mm longae, carinatae, carina glandulis paucis minutis sessilibus praedita. Racemi tandem lateraliter exserti, 4 mm longi, a pedunculis disarticulantes. Spiculae masculae involucretae, lineari-oblongae, 4 mm longae, dorso compressae, pallide virides; pedicelli breves, compressi, ad basin connati, pilis sericeis albis ad 2 mm longis dense barbati. Gluma inferior obtusa, membranacea, marginibus inflexis, 5-nervia, carinis dimidio superiore pilis 1—1.5 mm longis dense ciliatis. Spicula fertilis lanceolata, 3.5 mm longa; gluma inferior coriacea, superne bicarinata, glandulis paucis sessilibus praedita; lemma superius lineare, integrum, arista geniculata, 10 mm longa; columna contorta, minute scabra, 4 mm longa. Spiculae neutrae pedicellatae, lanceolatae, subacutae, 2.7 mm longae; pedicelli 2.5 mm longi, scabridi, apicem versus pilis longis ad basin tuberculatis obtecti; gluma inferior elliptica, 5-nervia, carinis parce glanduliferis.

Distr. Lesser Sunda Islands: Sumba Island, Milolo, Monod de Froideville 2012 (type, in Herb. Bogor.).

Ecol. In groups among the grass-vegetation on the shallow soil of a limestone plateau at 50 m altitude, a range for livestock and subjected to annual burning.

Note. This species is most closely related to the Australian *Iseilema ciliatum* C. E. Hubbard in Hook. Ic. Pl. (1935) 3286, up till now the only species described with ciliate hairs along the keels and tips of the involucre spikelets. Moreover the Sumbanese species has the tubercle-based hairs along the margins of the culm-blades, mentioned by S. T. BLAKE (1938). The species differ in the shape of the inflorescence: narrow and elongate in *I. minutiflorum*, dense and contracted in *I. ciliatum*. They particularly differ in the size of the spikelets:

	<i>I. ciliatum</i>	<i>I. minutiflorum</i>
pedicels of involucre spikelets	1.5 mm	0.5 mm
involucre spikelets	5—5.5 mm	4 mm
sessile spikelet	7 mm	3.5 mm
pedicels of pedicelled spikelets	3.5 mm	2.5 mm
pedicelled spikelets	3—3.5 mm	2.7 mm

POA L.

1. ***Poa luzoniensis*** Merr. in Philip. J. Sc. 1 (1906) Suppl. 180. Luzon (Merrill 4712).

This is *Poa pratensis*, probably escaped from cultivation as is the case in Java.

RIDLEY (1916) mentioned a specimen of *Poa luzoniensis* from New Guinea, leg. Boden Kloss, Utakwa Expedition. I saw this specimen in the British Museum Herbarium. On the label is written: "identical with a plant from the Java mountains, labelled *Poa annua* by Koorders (Tosari)". There are specimens of *Poa annua* L. from Tosari, they are, however, not identical with Kloss' specimen but true *Poa annua*.

RIDLEY (1916) wrote: "I have seen no Philippine specimens but the description by Merrill suits this plant". This is not exact. Merrill described a not tufted, erect perennial, with long creeping and branching rhizomes. His description manifestly points to *Poa pratensis* L. to which Hackel already hints. The specimen collected by Boden Kloss, however, is a tufted perennial without rhizomes. Most of the florets have fallen out, no perfect spikelet is present. It most probably is a mature specimen of *Poa brassii* Hitchc. in Brittonia 2 (1936) 110.

PSEUDORAPHIS Griff.

After Hitchcock accepted *Pseudoraphis* Griff. Not. Pl. Asiat. 3 (1851) 29 as distinct from *Chamaeraphis*, Miss A. Chase published the combination *Pseudoraphis squarrosa* (L. f.) Chase in J. Arn. Arb. 20 (1939) 313.

Miss VICKERY (1950) holds the view, that *Pseudoraphis spinescens* (R. Br) Vick. is the correct name for this species. She has doubts about the genuineness of the Linnean specimen and in her opinion R. Brown has "deliberately referred to the Linnean specimen but left out a reference to the description of Linnaeus f.". She also finds this description wrong in certain characters. The latter point is, to a certain extent, irrelevant for nomenclature, as typification is, in the presence of specimens, based on the identity of the latter only.

However, there seems to be no doubt whatever as to the genuineness of the Linnean specimen. R. BROWN (1810) referred *Andropogon squarrosus* L. f. to his *Panicum abortivum*. STAPF (1906) equally admits that the Linnean specimen is correctly identified by R. BROWN. HITCHCOCK saw the plant in the Linnean Herbarium. Miss A. Chase kindly sent me a copy of his note: "*Andropogon squarrosus* L. f. Specimen in Linn. herb. is labelled "*Andropogon scabrum*" with short description in Latin by Koenig. Label is pinned to sheet. Sheet has at left lower corner "Koenig", at middle "*Andr. scabrum*" (*scabrum* with 2 pencil marks through it). At right in pencil "*squarrosus*" J. E. S." (mith). The specimen consists of 4 upper parts of culms with 1—3 leaves and panicles 3—4 in. long. This is *Chamaeraphis squarrosus* (L. f.) Chase. Munro in Proc. Linn. Soc. Bot. 6 (1862) 53 says this Koenig specimen is *Chamaeraphis hordacea* R. Br. which it is not." A. S. H. 1930.

Finally SAVAGE (1945) definitely states that the Linnean specimen was examined by J. E. Smith and that the original label of Koenig as collector, as quoted by Linnaeus f. is attached to this sheet. Therefore there seems to be no doubt, that Miss Chase rightly accepted *Andropogon squarrosus* L. f. Suppl. (1781) 433 as the basonym of her combination.

VETIVERIA Bory.

The genus *Vetiveria* differs only slightly from *Chrysopogon*, the first genus having several-jointed racemes, the latter only 1-jointed racemes, consisting of a triplet of spikelets at the end of an usually long branch. This differential character holds only to a certain degree, as there are species with the lower racemes several-jointed, whereas the upper or the secondary branches bear 1-jointed racemes. Consequently there is much difference of opinion in the literature about the generic disposition of some species.

The Australian *Chrysopogon elongatus* (R. Br.) Benth. var. *filipes* Benth. Fl. Austral. 7 (1878) 539 extends to Malaysia. The only specimens recorded up to now, are the Brass specimens 8460 from New Guinea.

REEDER (1948) described them as *Chrysopogon filipes* (Benth.) Reeder var. *arundinaceus* Reeder.

They differ from typical specimens in being much taller (100—150 cm) and more robust with longer panicle-branches, fewer-jointed racemes, the glumes of the sessile spikelets yellow below (rather than evenly purple throughout) and the second glume not mucronate but with an awn as much as 6 mm long.

I agree with S. T. BLAKE (1944) that *Chrysopogon elongatus* (R. Br.) Benth. var. *filipes* must be referred to *Vetiveria*.

Reeder's variety, therefore, should be called:

Vetiveria filipes (Benth.) C. E. Hubbard var. ***arundinacea*** (Reeder) Jansen, nov. comb.

LITERATURE

- BACKER, C. A. 1928. Handb. Fl. Java 2.
 BLAKE, S. T. 1938. Proc. Roy. Soc. Queensl. 49 : 89.
 BLAKE, S. T. 1944. Monographic Studies in Austr. Andropogoneae 1 : 12.
 BROWN, R. 1810. Prodr. Fl. Nov. Holl. : 193.
 BUSE, L. H. 1854. Pl. Jungh. : 346.
 CHASE, A. 1943. J. Arn. Arb. 24 : 79.
 DUPERREY, L. I. 1830. Voy. Bot. 2 : 133, t. 21.
 JUNGHUHN, F. W. 1845. Nat. Geneesk. Arch. Ned. Ind. 2 : 51.
 KNEUCKER, A. 1909. Bot. Zeitschr. : 15.
 MERRILL, E. D. 1906. Philip. J. Sci. 1, Suppl. : 374.
 MUELLER, F. von. 1889. Transact. Roy. Soc. Victoria 1, 2 : 38.
 REEDER, J. 1948. J. Arn. Arb. : 360.
 RIDLEY, H. N. 1916. Transact. Linn. Soc. 9 : 251.
 SANTOS, J. V. 1944. J. Arn. Arb. 25 : 37.
 SANTOS, J. V. 1950. Nat. & Appl. Sci. Bull. 10 : 3—179.
 SAINT YVES. 1927. Rev. Bret. de Bot. 2 : 78, f. 100—103.
 SAINT YVES. 1928. Candollea 3 : 410—411.
 SAVAGE, S. 1945. Cat. Linn. Herb. : 181.
 STAPF, O. 1899. Kew Bull. : 117.
 STAPF, O. 1906. Kew Bull. : 348.
 STEUDEL, E. G. 1854. Syn. Pl. Glum. 1 : 315.
 VICKERY, J. W. 1940. Contr. N. S. W. Nat. Herb. 1, 2 : n. 13—17, 23—28.
 VICKERY, J. W. 1950. Proc. Roy. Soc. Queensl. 62 : 69.